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STUDIES ON FLOWER INITIATION IN BLACK CURRANT

I. SOME INTERNAL FACTORS AFFECTING FLOWERING

By T. A. A. NASR* and P. F. WAREING†
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THE process of flower initiation is clearly conditioned and controlled by a multiplicity of factors, of both internal and external origin. In most woody species, flower initiation exhibits a regular pattern both in space, in the restriction of flowers to certain morphologically distinct sites, and in time, in that flower initiation usually occurs at fairly distinct phases of the annual cycle of development of the shoot. The present paper describes a preliminary investigation into the possible nature of some of the internal factors determining these patterns of flower initiation in black currant (*Ribes nigrum*).

In this species, flower primordia are laid down in the axillary buds of the current year's shoot, in the year prior to that in which flowering occurs. The fact that flowers are formed only in the axillary buds, whereas the terminal bud of the shoot remains vegetative, suggests that correlative inhibition may be an important factor in flower initiation in this species. In other species, e.g. red currant (*Ribes rubrum*), flowers are borne mainly on spur shoots, which are axillaries of the 2-year or older long shoots. Since normal internode extension is absent in these spur shoots, here also it would appear that flower initiation occurs in axillaries which are partially inhibited.

Further evidence of the importance of correlative inhibition is seen in the effects of pruning ; for example, it is well known that in many species flowers are formed on an unpruned shoot, whereas, if the latter is cut back, buds which otherwise would have initiated flowers are stimulated to grow into vegetative long shoots, i.e. on being released from correlative inhibition they no longer initiate flowers.

On the other hand, in the Haden mango, the lateral buds remain inhibited in the presence of the terminal bud, but initiate flowers if the terminal buds are removed (Reece *et al.*, 1946). Similar effects have been observed in *Pinus sylvestris* (Wareing, 1953).

Since it is generally held that lateral buds are inhibited by auxin produced in the apical region of the main axis and since, further, it is known that only actively growing apices produce appreciable amounts of auxin, it would seem worth while to investigate whether the pattern of development of lateral buds is affected by the cessation of extension growth and the associated dormancy of the main axis.

Furthermore, it is known that the state of dormancy of the lateral buds themselves changes during the growing season, since the axillaries are capable of growing out when a shoot is decapitated early in the season, whereas if the shoot is pruned

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later in the summer the same buds remain dormant. It is thus important to know how far flower initiation is dependent upon the state of dormancy of the buds.

The following experiments were designed to elucidate these problems. Since, however, data were not available for the cycle of development of the annual shoot of black currant, observations were also carried out on the normal time and pattern of flower initiation, particularly in relation to other growth processes. The experiments deal with observations on the normal cycle of growth and flower initiation in the annual shoot of black currant, together with the effects on flower initiation and bud dormancy of various pruning treatments.

EXPERIMENT 1.

In this preliminary experiment 24 bushes of the variety Victoria were planted in open ground in January 1956. The shoots on these bushes were cut back to 2 or 3 buds to encourage the strong growth of new shoots. After growth had started, all except one of the newly formed lateral shoots were pruned off. Observations and measurements were designed to study the following points:

(1) The normal time of cessation of extension growth,
(2) The time of onset of dormancy of the lateral buds,
(3) The time of flower initiation, particularly in relation to the time of cessation of extension growth and dormancy of lateral buds.

Normal time of cessation of extension growth.

It was found that extension growth had stopped by about the end of July and the shoots had then formed terminal resting buds.

Time when axillary buds become dormant.

To investigate this aspect, a number of shoots were cut back 3 in. on the following dates, the number of shoots treated being given in the brackets: 4th July (21), 18th July (21), 1st August (13), 15th August (16). Similar shoots on the same bushes were marked as controls (21).

Observations made on the axillary buds of treated and untreated shoots showed that decapitation of shoots on 4th and 18th July resulted in outgrowth of the uppermost lateral shoots but much more lateral growth was produced by those decapitated on the former date. All buds of shoots decapitated on 1st and 15th August remained dormant.

Time of flower initiation.

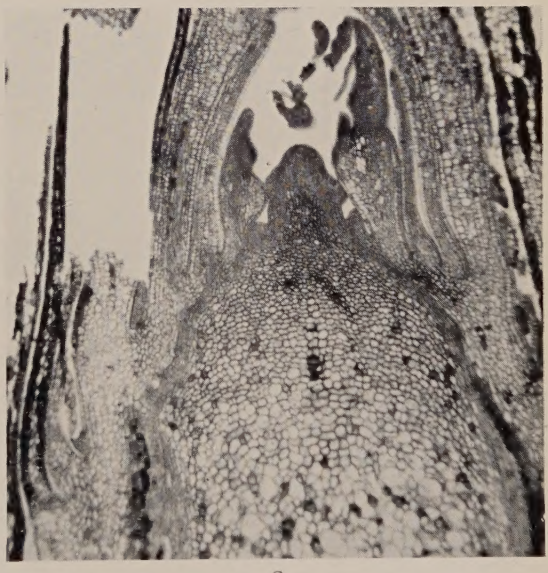
Sample buds were collected every two weeks between 4th July and 29th August from shoots left for this purpose. They were obtained as far as possible at the same level as the first axillary bud left after decapitation. The buds were kept in formalin-acetic-alcohol fixative for subsequent histological studies and were embedded and sectioned at a thickness of 8μ, using standard techniques. A modification of Sharman's technique (1943) was used for staining. The flattening and elongation of the apical meristem, and the concurrent appearance of flower primordia, were used as the criteria of flower initiation (Fig. 1).

The data of sampling given in Table I show that all buds were still vegetative on 1st August, but by 15th August 4 out of 21 buds showed flower primordia. On 29th August 12 out of 15 buds showed flower primordia.

PLATE I.

A

B



C

Fig. 1.
A, vegetative bud; B and C, flowering buds.

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TABLE I.

Dates of flower initiation in black currant, 1956.

Date of sampling	No. of buds collected	Vegetative	Flowering
4th July	24	24	0
18th July	24	24	0
1st August	24	24	0
15th August	21	17	4
29th August	15	3	12

The results of this experiment suggest that flowers are initiated in the axillary buds after extension growth has stopped, and that these axillary buds enter a state of partial dormancy (in the sense that they will not grow out after decapitation) before flower initiation.

EXPERIMENT 2.

The preliminary investigation carried out in 1956 was repeated in 1957 in greater detail and with the following objectives in view:

(1) To determine the relation of the normal time of cessation of extension growth and the dormancy of buds to the normal time of flower initiation,
(2) To ascertain whether dormancy of the axillary buds occurs simultaneously throughout a given shoot, or otherwise,
(3) To study the growth of the axillary buds in relation to the cessation of extension growth and to flower initiation.

The same bushes were used for this experiment as in the preliminary experiment of 1956. The shoots were cut back to 2-3 buds as in previous years and the new growth was restricted to a single shoot.

Normal time of cessation of extension growth.

To determine more accurately the normal time of cessation of extension growth, 8 shoots were selected at random, one on each of 8 bushes, and the extension growth was measured every two weeks until it had stopped. The observations indicated that extension growth had stopped by 8th August.

Onset of dormancy in axillary buds.

In order to follow the onset of dormancy in buds of different ages, the shoots were cut back to three different levels, viz. to 6, 12, and 18 nodes from the base, on 11th and 25th July and on 8th and 23rd August. The number of shoots in each treatment was 8, the treatments being distributed at random among the various bushes. The axillary buds on treated and untreated shoots were examined from time to time to ascertain whether the buds expanded or remained dormant. The results may be summarized as follows:

(1) None of the buds on the shoots cut back to 6 nodes expanded following decapitation on any of the dates, i.e. they appeared to be already dormant by 11th July.

(2) With the shoots cut back to 12 nodes, the uppermost axillaries elongated into very short laterals on the shoots cut on 11th July, but they remained dormant on shoots decapitated on the later dates.

(3) Buds on the shoots cut back to 18 nodes on 11th July grew out into well developed lateral shoots, whereas when cut back on 25th July only very short laterals were formed. With shoots similarly treated on 8th and 23rd August, all buds remained dormant.

Thus, it appears that the lateral buds enter dormancy progressively, the oldest ones in the basal region becoming dormant first and the upper younger ones later. The onset of dormancy of the buds appears not to be directly related to the cessation of extension growth since the lowermost buds were already dormant by 11th July, whereas extension growth continued for about 2 weeks after this date.

Growth of axillary buds.

In order to study the growth of axillary buds in relation to the cessation of extension growth and to the time of flower initiation, the lengths and widths of sample buds taken from extra shoots left for this purpose were measured. This was done at intervals of two weeks on 11th and 25th July, 8th and 22nd August, 5th September, and after 4 weeks on 3rd October. For each sample, the lengths and widths of all the buds from base to tip of several shoots were measured.

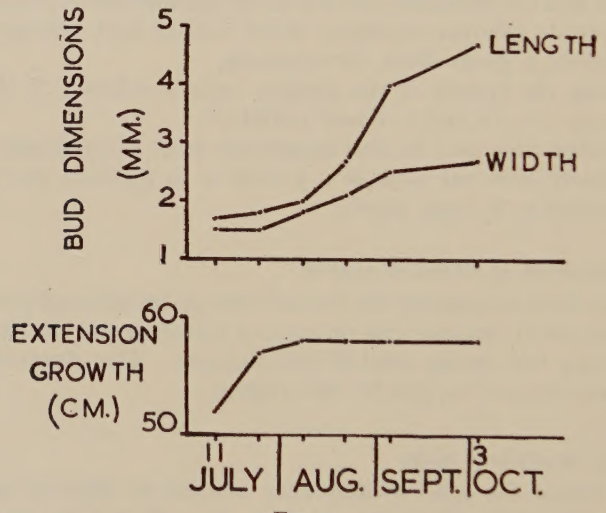

Fig. 2.
Growth of axillary buds, in relation to extension growth, in 1957.

The growth of the axillary buds during the course of the experiment is illustrated in Fig. 2. It is evident that there was a considerable growth of the buds, following the cessation of extension growth at about the end of July. This suggests that when the main shoot apex ceases active extension growth, the lateral buds are at least partially released from correlative inhibition, although they do not grow out into shoots.

Time of flower initiation.

Samples of buds at nodes 6, 12 and 18 on untreated control shoots were collected at intervals and preserved in F.A.A. fixative for sectioning. The technique for embedding, sectioning and staining was the same as in the previous year.

Table II.

Dates of flower initiation in black currant in 1957.

	Number of buds					
	Node 6		Node 12		Node 18	
	V	F	V	F	V	F
11th July	6	0	6	0	6	0
25th July	6	0	6	0	6	0
8th August	12	0	12	0	12	0
22nd August	12	0	8	4	3	9
5th September ..	6	0	2	10	1	11

V, vegetative bud; F, flowering bud.

The number of flower buds at the three different levels of control shoots is given in Table II. The data show that buds at all three levels remained vegetative up to 8th August. On 22nd August, however, a proportion of the buds at nodes 12 and 18 showed flower primordia, whereas those at node 6 were vegetative. On 5th September, nearly all buds at nodes 12 and 18 showed flower primordia, while all those at node 6 remained vegetative.

Bud development.

The development of the buds at the three different levels throughout the period of the experiment was followed by embedding and sectioning samples collected at intervals from control shoots.

The bud is borne on a short stalk and above this arises a series of bud scales and leaf primordia, spirally arranged. The number of scales or leaf primordia present in the median section was counted for the buds at each level on the successive dates and the results are shown in Table III. It is seen that about 20 scales or primordia were already present in the lowermost buds on 11th July, and this number had increased to only about 23 on the latest date, i.e. apical activity in the lowermost buds had almost ceased by the first date of sampling. This observation agrees with the fact that such buds were already dormant at that date. On the other hand, the uppermost buds had only 11 scales or primordia at the time of the first decapitation, and this increased to 19 by the date of the latest sampling (5th September). Evidently, the apices of the uppermost buds were still active for a considerable time after the first decapitation, which agrees with the observation that decapitation at the 18th node on 11th and 25th July resulted in outgrowth of the lateral buds.

Measurements were also made of the external dimensions of the buds on the various dates of treatments. The growth of the buds at the different levels is shown

TABLE III.

Number and length of scales and leaf primordia in median sections of buds at three different levels in 1957.

Date of sampling	Node 6			Node 12			Node 18		
	No. of buds examined	Leaf and scale primordia		No. of buds examined	Leaf and scale primordia		No. of buds examined	Leaf and scale primordia	
		Av. no.	Mean length (mm.)		Av. no.	Mean length (mm.)		Av. no.	Mean length (mm.)
11th July	6	19·9	2·1	6	14·3	1·5	8	11·0	1·2
25th July	6	19·5	2·1	7	14·3	1·5	8	11·8	1·5
8th Aug.	10	20·5	2·3	11	15·0	1·8	8	14·6	1·5
22nd Aug.	6	21·7	2·9	11	18·1	2·0	12	15·9	2·0
5th Sept.	7	22·7	3·2	7	20·3	3·1	11	19·2	2·6

in Table IV. It is seen that there is a marked increase in size at all levels, particularly following the cessation of extension growth of the main axis.

As already indicated, apical activity in the lowermost buds had almost ceased by the first date of treatment (11th July). Since these buds also showed a considerable increase in overall size following cessation of extension growth, observations were made to determine the origin of this increase in size. The length of leaf primordia at the three different levels was measured and the data are presented in Table III. It is seen that there was a considerable increase in length of leaf primordia after cessation of extension growth. These results show clearly that growth in size of the lowermost buds was mainly due to this increase in size of the bud scales and leaf primordia, since very few new primordia were formed.

It is also evident that the increase in size of buds at the 18th node was partly due to the increase in number of leaf primordia laid down by the apical meristems and partly to the increase in the size of the bud scales and leaf primordia (Tables III and IV). The behaviour of the buds at the 12th node appeared to be intermediate between that at the 6th and the 18th node.

EXPERIMENT 3.

The following experiment was carried out to test the hypothesis that, when the main shoot axis ceases active extension growth, the lateral buds are partially released from correlative inhibition. Plants of the variety Baldwin, raised from hardwood cuttings and grown in 7-in. pots, were selected for uniformity and divided into two groups of 5 plants each, which were then exposed to the following photoperiodic conditions:

(1) 8-hour photoperiods (" short day "),
(2) 24-hour photoperiods (" continuous illumination ").

Measurements of bud dimensions (length and width) were made before the treatments began on 30th May and were continued every two weeks until 25th July, after which date the experiment was discontinued.

TABLE IV.

Development of buds in black currant at three different levels in 1957.

Date of sampling	Nodes 1-6			Nodes 7-12			Nodes 13-18			Nodes above 18th		
	No. of buds measured	Length	Width	No. of buds measured	Length	Width	No. of buds measured	Length	Width	No. of buds measured	Length	Width
11th July	25	2·7	2·0	48	2·3	1·75	48	1·6	1·3	12	1·0	0·75
25th July	42	2·5	2·0	69	2·0	1·8	65	1·5	1·4	53	1·2	0·94
				(Extension growth ceased about the end of July)								
8th Aug.	40	2·7	2·2	72	2·6	2·1	71	2·0	1·8	49	1·3	1·3
22nd Aug.	49	3·3	2·4	72	3·2	2·3	69	2·5	2·1	50	1·9	1·7
5th Sept.	40	4·4	2·8	68	4·7	2·8	69	3·8	2·4	64	3·2	2·1
6th Oct.	47	4·7	2·9	60	5·4	3·0	56	4·8	2·7	71	4·0	2·6

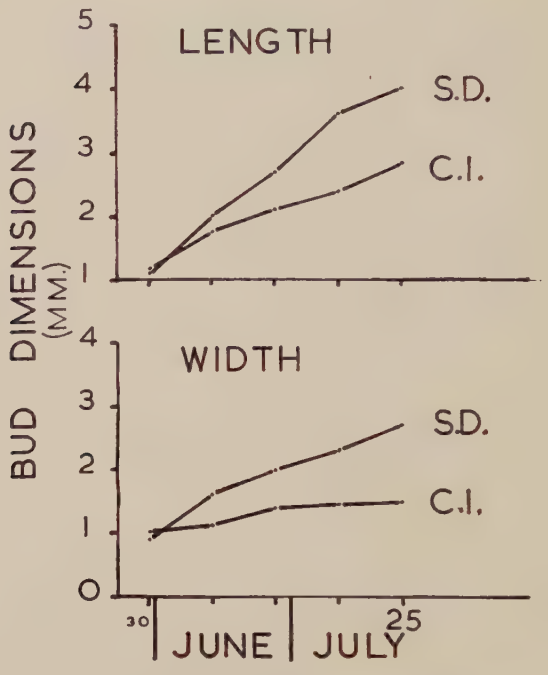

Fig. 3.
Development of buds under short days and continuous illumination.
S.D., short days; C.I., continuous illumination.

Extension growth ceased in the short-day series about 2 weeks after the commencement of the treatment. It was found that the growth of the buds was stimulated by short days as compared with continuous illumination (Fig. 3). These results agree with the observation that under field conditions bud growth proceeds actively when extension growth ceases. These observations support the hypothesis that, when the main shoot apex ceases active extension growth, the lateral buds are at least partially released from correlative inhibition, so that they increase in size even though they do not grow out into shoots.

DISCUSSION.

The foregoing experiments suggest a number of inter-relations between the cessation of extension growth, the onset of bud dormancy and flower initiation.

Evidently the lateral buds in black currant are at first held in check by normal correlative inhibition, since decapitation early in the growing season, when the buds are young, causes them to grow out. As such buds get older, however, they fail to grow out following decapitation, indicating that they gradually enter a state of dormancy. The onset of dormancy seems to be a function of the age of the individual bud, since this dormancy is most advanced in the basal regions and occurs in the buds of the more distal regions later in the season. This onset of dormancy of the lateral

buds explains why they fail to grow out on being released from the inhibition by the main shoot meristem when the latter enters dormancy. It is clear that the buds show a progressive increase in dormancy and that at certain stages it can be described as " partial dormancy " in so far as such buds do not expand following decapitation, although the apical meristem within is still active and initiating leaf primordia. At a still later stage, the apical meristem itself becomes dormant but the leaf primordia and bud scales are still capable of further growth. The buds of the basal region have evidently already reached the latter stage at the time of cessation of extension growth. On the other hand, the buds at higher nodes are still exhibiting activity of the apical meristem at this time and it is these buds which initiate flower primordia.

Although the lateral buds do not normally grow out following the cessation of extension growth, nevertheless the observations on bud growth seem to indicate that there is a very marked stimulation of growth when the main shoot apex enters dormancy. This would suggest that the lateral buds are indeed released from apical dominance at this time but, because of their own partial dormancy, they are unable to expand and resume active extension growth. If the apical meristem of the bud has already ceased activity at the time of cessation of extension growth, it is evident that only growth of bud scales and leaf primordia is possible. On the other hand, if the bud meristem itself is not yet dormant, it seems that the general stimulus arising from cessation of extension growth results in its transformation from the vegetative to the flowering condition. It has been observed that flower initiation follows the cessation of extension growth also in raspberry (Williams, 1959), suggesting that the results obtained with black currant may be applicable to other species.

From the present investigation, therefore, it would appear that as long as the main shoot axis is continuing active extension growth, the axillary buds remain too inhibited to permit flower initiation. If the shoots are decapitated at this time, the axillary buds grow out as vegetative shoots. When, however, a state of partial dormancy is established, the axillary buds are still capable of flower initiation but require release from correlative inhibition in order to do so. If they are not released from correlative inhibition before the bud apical meristem itself becomes dormant, they are no longer capable of initiating flowers. Thus the conditions necessary for flower initiation appear to lie within certain narrow limits.

SUMMARY.

1. The inter-relations between extension growth, bud development, bud dormancy and flower initiation were studied in the black currant, var. Victoria. In this variety, extension growth ceases at the end of July or early in August. Flower initiation occurs during the third and fourth weeks of August.

2. The state of dormancy of the axillary buds was tested at intervals by determining whether they grew out following decapitation of the main axis. Early in their development the buds are non-dormant in that they are able to grow out when released from correlative inhibition, but they later enter a state of partial dormancy, so that they will not now expand in response to decapitation.

3. Even after the lateral buds enter this state of partial dormancy, the apical meristems of the upper lateral buds are still capable of further activity for a time.

4. Following the cessation of extension growth, there is a considerable stimulation of bud growth and, in the upper buds, this is accompanied by the transition of the meristem from the vegetative to the flowering condition. In the lower buds, however, the apical meristem has by this time become fully dormant so that these buds fail to initiate flower primordia.

5. The internal conditions for flower initiation appear to be the release of the lateral buds from correlative inhibition and a state of partial dormancy of the buds.

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STUDIES ON FLOWER INITIATION IN BLACK CURRANT

II. PHOTOPERIODIC INDUCTION OF FLOWERING

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OBSERVATIONS on the normal developmental cycle in black currant (Nasr and Wareing, 1961) have shown that flower initiation occurs immediately after cessation of extension growth, suggesting that possibly there is a causal relationship between the two phenomena. If this hypothesis is correct, then any treatment which induces cessation of extension growth ought to promote early flower initiation. Black currants are known to be sensitive to photoperiodic conditions, short days bringing about early cessation of extension growth (Hoyle, 1955), but there have been no previous reports of induction of flowering in black currant by photoperiodic treatment. Experiments were, therefore, carried out to test the hypothesis that short-day conditions may indirectly promote flowering by inducing the cessation of extension growth. A preliminary report of this work has already been published (Nasr and Wareing, 1958).

It was suggested in a previous paper (Nasr and Wareing, 1961) that flower initiation may depend on the release of the buds from correlative inhibition when the main apical meristem becomes dormant. It was shown, however, that whereas lateral buds released from correlative inhibition early in the season grow out into vegetative shoots, somewhat later they lose this capacity to expand, even though they increase considerably in size following the cessation of extension growth. These observations suggested that flower initiation may depend on two conditions, viz. (1) release from correlative inhibition, and (2) partial dormancy of the buds. It is thus necessary to consider how far the capacity of a bud to initiate flowers is dependent upon its state of dormancy. Now it is known that photoperiodic conditions have a marked effect on bud dormancy (Wareing, 1956). Hence, manipulation of photoperiodic conditions would appear to offer a further possible technique for studying the conditions necessary for flower initiation.

Experiments were also carried out to determine how far seasonal changes in day-length conditions may be important in the annual developmental cycle in black currant under natural conditions.

The conditions necessary for the breaking of dormancy of black currant buds were also investigated.

Material and methods.

The black currant plants used in these experiments were raised from hardwood and softwood cuttings.

Tungsten lamps were used to extend day-length in summer but during winter, when the natural daylight was of low intensity, fluorescent lamps were used to

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increase light intensity. The short-day (" S.D.") plants received natural daylight between 8 a.m. and 5 p.m. The long-day (" L.D.") plants received natural daylight supplemented up to 10-11 p.m. by tungsten-filament or fluorescent lamps, whereas those exposed to continuous illumination received natural daylight supplemented between 5 p.m. and 8 a.m. by tungsten-filament or fluorescent lamps.

In experiments carried out under field conditions, the S.D. plants were put into a light-tight shed in the open without control of temperature. Where the experiments were carried out in a heated glasshouse, the S.D. plants were moved into light-tight compartments which were maintained at the general glasshouse temperature.

Experiment 1.

This experiment was carried out in 1957 to test the hypothesis that flower initiation is dependent on the cessation of extension growth and that treatments which bring about the latter may also induce flowering.

Plants of the variety Baldwin raised from hardwood cuttings were allowed to grow under natural long-day conditions until they had attained a height of about 50 cm., and were then selected for uniformity and divided into three groups which were exposed to the following photoperiodic conditions:

(1) 8-hour photoperiods (29 plants),
(2) 18-hour photoperiods (19 plants),
(3) Natural day-length conditions (10 plants).

The experiment was carried out in the open. The treatments began on 21st June, and within $2\frac{1}{2}$-3 weeks the plants under S.D. had ceased extension growth. On 29th July (after 5 weeks of treatment), 14 of these S.D. plants were transferred back to L.D., under which conditions most of the axillary buds (except a few in the basal region of the new wood) expanded in 2-3 weeks ; a high proportion of the axillaries in the upper part of the shoots produced flowers, which set fruit in September.

The plants maintained under L.D. throughout continued active extension growth until the experiment was terminated on 12th September. At this time many of the axillary buds had elongated into short shoots which were entirely vegetative.

The plants maintained under natural day-length conditions ceased extension growth at the beginning of August and by the following spring had initiated flowers in the normal way.

From these results it is evident that S.D. promotes flowering, but it is not clear whether photoperiodic treatment promotes flowering independently of any effects on extension growth, or whether flower initiation is an indirect effect resulting from cessation of extension growth. The results also indicate that buds formed under S.D. could easily be induced to break dormancy by exposure to L.D., the buds resuming growth in about 2-3 weeks.

The experiment was repeated with the variety Seabrook's Black and similar results were obtained.

Experiment 2.

This was carried out to obtain further evidence as to whether there is direct photoperiodic induction of flowering under S.D., or whether flower initiation is primarily a response to the cessation of extension growth which occurs under S.D.

In the previous paper of this series it was postulated that flower initiation in black currant depends upon release of the lateral buds from correlative inhibition when the main apical meristem becomes dormant, and upon partial dormancy of the buds so that they do not expand when released from inhibition in this way. If this hypothesis is correct, it might be expected that experimental decapitation of the shoots would promote flower initiation even under L.D., provided that the buds were partially dormant, so that they would not expand following decapitation. Accordingly, plants previously grown under L.D. were decapitated (a) at the commencement of the experiment, and (b) after exposure to 16 S.D. It was known that a period of 16 S.D. is insufficient to bring about the complete cessation of extension growth and the formation of terminal resting buds, but it was thought that this prior treatment might increase the dormancy of the lateral buds, so that they would be less likely to grow out after decapitation.

Since it is known that photoperiodic induction of flowering in herbaceous plants depends upon the presence of mature leaves (Moshkov, 1936 ; Cailachjan, 1936), the effect of defoliation of half of the plants was studied in conjunction with decapitation and photoperiodic treatments.

The plants (variety Baldwin) were raised from softwood cuttings which had been taken in June. When the cuttings had rooted, they were potted into 5-in. pots and allowed to grow under L.D. in a house maintained above 60° F. until they had attained a height of 40-50 cm. The particulars of the experiment, which was started on 8th October, are shown in Table I. The plants were divided into 8 equal groups of 10 plants each.

Effects on dormancy.

The uppermost buds of plants decapitated at the beginning of the experiment grew out under L.D., whether with or without leaves. Of the corresponding plants put under S.D., only the buds of those without leaves grew out and these very shortly ceased growth again, after partial expansion of the leaves. On the other hand, the buds on those plants retaining their leaves remained dormant during S.D. treatment, but expanded on subsequent transfer to L.D.

In plants exposed to initial S.D. treatment before decapitation, most buds

Table I.

Effects of decapitation, defoliation and photoperiod on flowering of black currant (var. Baldwin).

Decapitated (*ca.* 2 in. removed) at beginning of experiment				Intact, under S.D. (9 hrs.) for 16 days, then decapitated			
Not defoliated	Defoliated	Not defoliated	Defoliated	Not defoliated	Defoliated	Not defoliated	Defoliated
L.D. (15-16 hrs.) throughout	L.D. throughout	S.D. (9 hrs.) for 28 days, then L.D.	S.D. for 28 days, then L.D.	L.D. throughout	L.D. throughout	S.D. for 18 days, then L.D.	S.D. for 18 days, then L.D.
All 10 plants vegetative	All 10 plants vegetative	6/10 plants flowered	All 10 plants vegetative	5/10 plants flowered	6/10 plants flowered	5/10 plants flowered	5/10 plants flowered

in the upper two-thirds of the shoot grew out on exposure to L.D., whether transferred to L.D. immediately following decapitation or after a further 18 S.D. treatment. Thus, preliminary treatment with S.D. did not reduce the ability of the buds to grow out when subsequently transferred to L.D.

Effects on flowering.

Exposure to S.D. in all cases resulted in some flowering (Table I), except in the plants defoliated at the same time as decapitation and followed immediately by S.D. treatment. In no group did more than 6 out of 10 plants initiate flowers. This relatively poor flowering response may be due to the fact that this experiment was carried out during the winter when the light intensity was low, despite supplementary illumination from fluorescent lamps.

It is clear that decapitation in conjunction with L.D. conditions does not bring about flower initiation but simply stimulates the lateral buds to grow vegetatively. On the other hand, prior exposure to 16 S.D., followed by decapitation and exposure to L.D., did result in flowering. It had been assumed, at the beginning of this experiment, that exposure of the *intact* plants to 16 S.D. would not be sufficient to induce flowering, since this duration of S.D. treatment does not bring about cessation of extension growth. The results of the next experiment, however, indicated that this assumption was not correct, and hence it cannot be deduced that the flowering of plants exposed to 16 S.D. before transfer to L.D. conditions was primarily due to the effect of decapitation. On the other hand, the observation that flowering occurred only in those plants which retained their leaves during exposure to S.D. indicates that the conditions necessary for flowering in black currant are directly comparable with those for photoperiodic induction of flowering in herbaceous species, and suggests that S.D. treatment has, indeed, a direct effect on flower initiation in black currant, independent of any effect on extension growth. The following experiment was carried out to obtain further evidence on this question.

Experiment 3.

The plants were raised from hardwood cuttings of the variety Baldwin and left to grow under L.D. conditions until they had attained a height of 50-60 cm. Twenty-four plants which were selected for uniformity were given 16 S.D. (from 30th May to 15th June), after which half of them were decapitated (about 2 in. of the shoot removed) and the other half left intact. All plants were then immediately transferred to L.D.

By 22nd July all decapitated plants and 9 out of 12 intact ones had produced flowers. After the initial exposure to 16 S.D. the intact plants had not formed terminal resting buds, and they resumed active extension growth after transfer back to L.D. conditions.

These results suggest that S.D. treatment may have a direct effect on flower initiation independently of any effect on extension growth.

Experiment 4.

The preceding experiment was repeated, but instead of 16 S.D. the plants were given only 8 S.D., after which period 7 were left intact and another 7 were decapitated. They were transferred immediately to L.D. and at this stage were about 60-70 cm. in length.

PLATE I.

Fig. 1.
A black currant shoot bearing both leaves and flowers. Note that the flowers are borne in clusters in the axils of leaves on the new growth. Photographed in January 1958.

[face p. 14

PLATE II.

FIG. 2.
Various types of flowering shoots in black currant.
A. The bud has elongated into a normal vegetative shoot bearing a cluster of flowers of the normal type.
B and C. The flowers are borne singly in the axils of reduced leaves (bracts) on the new growth.
(Photographed in August 1958.)

By 6th August none of the intact, but 5 of the 7 decapitated, plants had produced flowers. The non-flowering plants were kept under further observation to ascertain whether or not they flowered at a later date, but none of them did so. Thus, decapitated plants will flower in response to as few as 8 S.D., whereas intact plants require a longer period of S.D. treatment. This result supports the hypothesis that release of the lateral buds from correlative inhibition is a necessary condition for flower initiation in black currant. On the other hand, exposure to 16 S.D. induced flowering without decapitation, although such treatment was not sufficient to bring about the complete cessation of extension growth and the formation of terminal resting buds. Nevertheless, closer observation might reveal that there had been some arrest of growth after 16 S.D., with a consequent reduced inhibition of lateral buds.

These results, therefore, do not give a clear answer to the question as to whether there is a direct effect of photoperiodic conditions on flower initiation, i.e. one independent of the effect of S.D. in bringing about the cessation of extension growth.

Atypical flowering shoots.

Normally in black currants, some of the lateral buds elongate into leafy shoots without flowers, while others may give rise to very short laterals consisting of a basal rosette of leaves and a terminal, determinate inflorescence without leaves or pronounced bracts. It was found that with certain photoperiodic treatments an intermediate type of inflorescence was produced. The plants which were initially given 16 S.D., then decapitated and defoliated and transferred to L.D. (Table I, 3rd last column), bore this intermediate type of flowering shoot ; some buds grew out into an axis bearing leaves, with single flowers or short inflorescences in their axils (Fig. 1). Occasionally the lateral bud elongated into a more normal short shoot, with a terminal inflorescence which showed a reversion to the vegetative condition in the development of a leafy shoot by direct extension of the inflorescence axis, or of a branch thereof (Fig. 2).

Experiment 5.

In the previous paper (Nasr and Wareing, 1961) it was observed that, under field conditions, extension growth ceases about the end of July and is followed by initiation of flower primordia about mid-August. The question arises as to whether decreasing day-length in July plays a role in determining the time of cessation of extension growth and hence of flowering. To investigate this point, an experiment was carried out in 1958 with bushes of Victoria black currant grown in the open. Twelve of these were maintained under 17-hour photoperiods (corresponding to the natural photoperiod at mid-summer) and another 12 were left as controls under natural day-length. The treatments began on 14th July and continued till the end of September. Observations on the formation of terminal resting buds were carried out from time to time to ascertain whether there was any difference in the time of cessation of extension growth.

It was observed that, while the control plants ceased extension growth about the end of July, the plants maintained under 17-hour photoperiods continued to grow in length, producing new leaves until the end of September when the experiment was terminated.

These results would seem to indicate that decreasing day-length plays an important role in determining the cessation of extension growth in Victoria black currants about the end of July, under field conditions.

DISCUSSION.

It is evident from the results of the foregoing experiments that exposure to short days promotes flower initiation in black currants. The possibility that short days might promote flowering was suggested by the observation that under natural conditions flower initiation follows the normal cessation of extension growth and that short days rapidly bring about cessation of extension growth. Certain observations, however, suggest that photoperiodic conditions may have a direct effect on flower initiation in black currants, independently of any effect on extension growth. Thus, it was found that exposure to 16 short days was sufficient to induce flowering in intact plants, although these had not formed terminal resting buds at the end of such short-day treatment and rapidly resumed growth on transfer back to long-day conditions. Moreover, the observation that the presence of leaves is necessary for the induction of flowering in decapitated plants shows a direct parallel with the situation in herbaceous species, where there is strong evidence that short days may induce flowering independently of any effects on dormancy. The foregoing evidence thus suggests that short days may have a direct effect on flower induction in black currants. On the other hand, exposure to a period of 8 short days was not effective in inducing flowering in intact plants, but was partially successful if the plants were decapitated after such exposure. This observation indicates that experimental stopping of extension growth does, in fact, increase the sensitivity of the plants to photoperiodic treatment. Nevertheless, decapitation alone under long-day conditions is not effective in inducing flowering. It would seem that a decision on the question as to whether short-day treatment acts directly or indirectly cannot be arrived at on the basis of the available evidence and that further investigation is required.

It was previously suggested (Nasr and Wareing, 1961) that flower induction in black currant under natural conditions depends upon release of the lateral buds from correlative inhibition when the main apical meristem of the shoot becomes dormant, and upon partial dormancy of the lateral buds so that they do not expand fully at this time. It is possible that experimental decapitation provides the necessary release from correlative inhibition and that the presence of leaves under short-day conditions inhibits expansion of the buds so that the conditions necessary for flower initiation are provided.

From the results of Experiment 5 it would seem that, under natural conditions, seasonal changes in day-length may be important in determining the time of cessation of extension growth in black currants, and that these seasonal changes will therefore also effect flower initiation indirectly, even if there is not a more direct effect.

SUMMARY.

1. When actively growing plants of black currants var. Baldwin are transferred from long-day to short-day conditions, flower primordia are initiated in the lateral buds, whereas there is no flower initiation in plants maintained continuously under long-day conditions.

2. In intact plants flowers are initiated in response to 16 short days; in decapitated plants the duration of treatment can be reduced to 8 short days.

3. The presence of mature leaves is necessary for flower initiation in response to short days.

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A COMPARISON OF LIME-SULPHUR WITH AN ORGANIC-FUNGICIDE ALTERNATIVE IN THE APPLE SPRAY PROGRAMME

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Among the organic fungicides developed in recent years, captan has proved superior to most for the control of apple scab, *Venturia inaequalis* (Cke.) Wint., but ineffective against powdery mildew, *Podosphaera leucotricha* (Ell. and Everh.) Salm. On the other hand, only 2:4-dinitro-6-(1-methyl-*n*-heptyl)phenyl crotonate, dinocap,* has shown much merit against mildew (Moore and Kirby, 1952 ; Sprague, 1955 ; Groves *et al.*, 1958), although at the usually recommended rate, 0·025%, it could not be relied upon to control scab. Lime-sulphur controls both diseases but sometimes causes damage, so that milder forms of sulphur (colloidal, dispersible), though somewhat less effective, are often preferred. Both lime-sulphur and dinocap have acaricidal properties ; captan has not, and so is toxic neither to the fruit tree red spider mite, *Metatetranychus ulmi* (Koch), nor to mites predacious on it (Collyer and Kirby, 1955, 1959).

To replace sulphur sprays by combined sprays of captan and dinocap would enhance costs, but might prove economic in the long run if good control of scab, mildew, and red spider were accompanied by higher yields or superior fruit quality or both. The following experiments were undertaken to study these issues.

Trees and layout.

The experiments were conducted on a plot of summer-pruned dwarf-pyramid apple trees on M.VII rootstock, planted at 8 ft. by 4 ft. in autumn 1949 and comprising four 320 ft. rows of the dessert varieties Cox's Orange Pippin and James Grieve, and four rows of the culinary varieties Bramley's Seedling and Newton Wonder (Moore, 1954). Each experimental plot was a rectangle of six trees, three of each dessert or culinary variety randomized in adjacent rows, and was surrounded by similar trees of the scab-resistant variety, Edward VII, which served as a barrier to spray drift. The plan is illustrated in Fig. 1 (see p. 20).

COMPARISON OF DINOCAP WITH LIME-SULPHUR, 1951-52.

While the trees were becoming established, they were used to provide a preliminary comparison of dinocap, as a commercial 25% wettable powder at twice the recommended field strength (0·05% active ingredient), with lime-sulphur at 1%. Sprays were applied in both seasons at green-cluster, pink-bud, and petal-fall, but in 1952 a fourth application was made a fortnight after petal-fall. The treatments, including an unsprayed control, were randomized on single plots in each of eight blocks, four of dessert and four of culinary varieties.

* The commercial formulation is known as Karathane.

Table I.

Control of scab on foliage and fruit, and of mildew in fruit buds, 1951-52.

Variety	1951			1952		
	Lime-sulphur 1%	Dinocap 0·05%	Unsprayed control	Lime-sulphur 1%	Dinocap 0·05%	Unsprayed control
	Mean category (max. 5·0) for scab on foliage in July					
Cox's Orange Pippin ..	0·3	0·0	0·1	1·3	1·4	2·5
James Grieve	0·0	0·0	0·0	1·3	1·4	2·8
Bramley's Seedling ..	0·8	0·9	3·3	1·2	1·3	2·8
Newton Wonder ..	1·8	1·1	2·9	1·3	1·3	2·6
	Mean percentage no. of fruits scabbed at harvest					
Cox's Orange Pippin ..	0·0	6·9	11·4	5·5	4·4	60·9
James Grieve	0·1	5·0	15·2	2·4	9·2	29·6
Bramley's Seedling ..	4·6	15·4	20·8	2·9	12·5	20·0
Newton Wonder ..	9·5	5·3	48·9	5·6	0·0	31·3
	Mean percentage no. of fruit-buds mildewed in following spring					
Cox's Orange Pippin ..	7·9	7·2	13·6	1·2	1·3	3·2

The data (Table I) indicate that dinocap was the less persistent spray. Although as effective as 1% lime-sulphur against foliage scab in July, it was, except on Newton Wonder, inferior on the irregular first crops on these young trees. Both treatments gave moderate control of mildew.

Evidently dinocap alone, even at double the recommended rate, would be unreliable for good scab control, and the second experiment was therefore designed to study the effects of adding " half-strength " captan, 0·05%, to dinocap at both normal and double rate in comparison with lime-sulphur.

COMPARISON OF DINOCAP PLUS CAPTAN WITH LIME-SULPHUR, 1954-56.

Materials and methods.

Sprays were applied by hand-lance from a mobile spraying machine, giving 200-250 lb./sq. in. pressure, at pink-bud, petal-fall, and two weeks later. The treatments were randomized on double plots, and there were four replications on dessert and four on culinary varieties.

The treatments were:

1. Lime-sulphur, 2% v/v pre-blossom and 1% v/v post-blossom,
2. Dinocap, 0·05%,
3. Dinocap, 0·05% plus captan 0·05%,
4. Dinocap, 0·025%,
5. Dinocap, 0·025% plus captan 0·05%.

Dinocap was used as a 25% wettable powder as before, and captan as a commercial 50% wettable powder. To avoid undue mortality among predators of the fruit tree red spider mite, insecticides were confined to lead arsenate and nicotine with wetting agent.

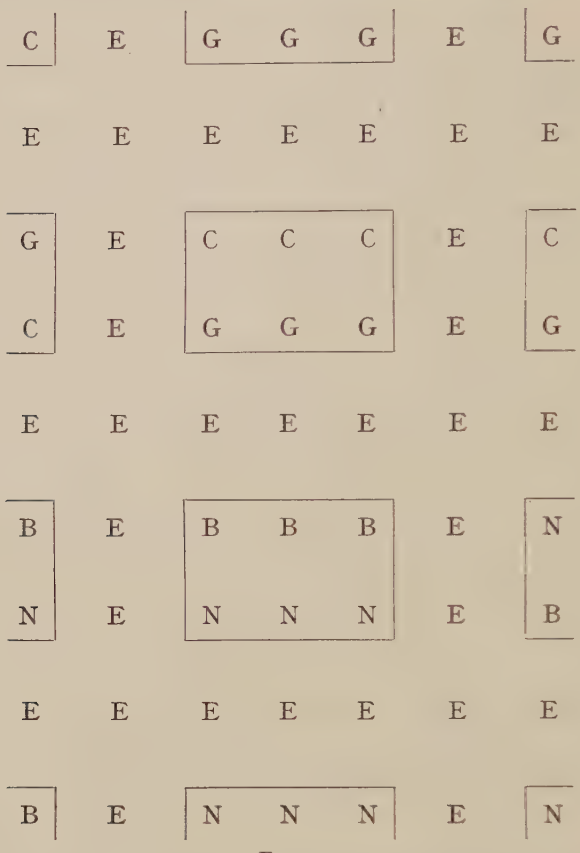

FIG. 1.
Specimen spray plots.
C, Cox's Orange Pippin; G, James Grieve; B, Bramley's Seedling; N, Newton Wonder; E, Edward VII.

Records were made as follows:

Apple scab: as category records on foliage (Moore, 1930), and as percentage number of fruits infected per tree.

Apple mildew: as percentage number of leaves infected on 10 random extension shoots per tree.

Fruit tree red spider mite: as numbers of mites and eggs recorded from mangling a sample of 8 leaves per tree between absorbent paper (Austin and Massee, 1947).

Fruit russet: as percentage number of fruits affected, or as a severity index (% × mean grade) (Moore and Pearce, 1946).

Crop: as numbers of fruits (set or mature) per 100 blossom trusses, and as crop weights in lb./tree.

Some of the data were transformed for analysis: percentages and numbers of fruits/100 blossom trusses to angles of equal information, and mite data to log $(n + \frac{3}{8})$. Transformed values are shown in the tables in italics. With few exceptions (Table VII), only data showing significant differences are presented.

Results.

Apple scab.

In 1955 and 1956 lime-sulphur was the most effective foliage treatment (Table II), but in 1954 it was inferior to the dinocap/captan mixture. Dinocap alone showed some control as it was almost invariably more effective at 0·05% than at 0·025%. The addition of captan greatly improved control in 1954 ($P < 0·001$), but was less beneficial in the later years.

Table II.

Control of foliage scab ; mean category values per tree in summer (max. 5·0).

Season	Variety	Lime-sulphur	Dinocap with captan*		Dinocap without captan		Sig. diff. P=0·05
			0·05%	0·025%	0·05%	0·025%	
1954	C.O.P.	0·6	0·2	0·1	1·0	1·4	0·33
	B.S.	1·2	0·5	0·3	1·7	1·9	0·29
1955	C.O.P.	1·5	1·8	2·0	2·0	2·3	0·25
	J.G.	0·3	0·0	0·5	0·3	0·8	0·36
	B.S.	1·4	1·6	1·9	1·7	2·2	0·28
	N.W.	1·7	1·8	2·2	2·0	2·4	0·45
1956	C.O.P.	1·1	2·0	2·3	2·2	2·8	0·43
	B.S.	1·4	2·0	2·3	1·9	2·2	0·56
	N.W.	0·5	1·7	1·9	1·3	1·8	0·33

* 0·05% captan.

Most infection of fruit (Table III) occurred where dinocap was applied at 0·025% alone. The addition of captan gave greater improvement in control than doubling the strength of the dinocap.

Table III.

Control of fruit scab ; mean percentage number of scabbed fruit per tree.

Season	Variety	Lime-sulphur	Dinocap with captan*		Dinocap without captan		Sig. diff. P=0·05
			0·05%	0·025%	0·05%	0·025%	
1954	C.O.P.	1·5	0·7	1·1	5·4	9·6	
		7·1†	*4·6*	*5·9*	*13·4*	*18·0*	*3·10*
	B.S.	3·8	0·7	1·3	3·0	19·7	
		11·2	*4·6*	*6·5*	*9·9*	*26·3*	*9·75*
1956	C.O.P.	21·5	27·2	34·4	45·9	67·0	
		27·6	*31·4*	*35·9*	*42·6*	*54·9*	*15·68*
	J.G.	0·9	0·6	1·2	2·3	3·0	
		5·4	*4·6*	*6·2*	*8·6*	*9·9*	*3·73*
	B.S.	22·8	23·7	22·5	33·8	56·3	
		28·5	*29·1*	*28·3*	*35·5*	*48·6*	*5·84*
	N.W.	2·1	4·0	7·9	10·0	17·5	
		8·3	*11·5*	*16·3*	*18·4*	*24·7*	*4·38*

* 0·05% captan. † Data in italics transformed, see p. 20.

Although lime-sulphur gave control insignificantly different from that obtained with the best combination of the organic sprays, it was relatively less effective on the fruit as well as on the foliage (Table II) in 1954 than in the later years. The April rainfall in 1954 was exceptionally low (0·03 in. from 7th to 30th ; Trowell, 1955), and as the pre-blossom sprays may therefore have contributed little that year to any of the spray programmes, the reduced relative effectiveness of lime-sulphur was probably due to the lower strength used in post-blossom applications.

The varieties James Grieve and Newton Wonder were less scab-susceptible than Cox's Orange Pippin and Bramley's Seedling under these experimental conditions.

Apple mildew.

As seen in Table IV, the evidence in favour of doubling the strength of dinocap for mildew control is not convincing on these dwarf-pyramid trees. The addition of captan had no appreciable influence, and lime-sulphur was as effective as any of the other treatments.

TABLE IV.

Control of foliage mildew ; mean percentage number of infected leaves per tree in summer.

Season	Variety	Lime-sulphur	Dinocap with captan*		Dinocap without captan		Sig. diff. P=0·05
			0·05%	0·025%	0·05%	0·025%	
1954	C.O.P.	33·0	32·3	36·9	30·5	38·7	
		35·1†	*34·6*	*37·3*	*33·4*	*38·5*	*3·20*
1956	C.O.P.	13·9	10·8	15·8	11·2	16·9	
		21·7	*19·1*	*23·3*	*19·5*	*24·0*	*4·83*
	J.G.	10·8	9·3	14·0	10·6	12·2	
		19·2	*17·8*	*22·0*	*19·0*	*20·4*	*2·24*

* 0·05% captan. † Data in italics transformed, see p. 20.

Fruit tree red spider mite.

The data are set out in Table V. Spraying had ceased in early June and, by July and sometimes August, dinocap, particularly at 0·05%, was still showing better control than lime-sulphur. The differences were reduced as natural pest/predator equilibrium was gradually restored ; in 1954 the higher red spider populations associated with lime-sulphur sharply declined, and in 1956 the lower levels associated with dinocap increased. The effect of including captan sometimes just reached significance, but was not always beneficial.

Spray damage.

As shown in Table VI, the culinary varieties, and especially Bramley's Seedling, developed little russeting, but Cox's Orange Pippin and, in one instance, James Grieve were more russeted by lime-sulphur than by any other treatment. More

russeting occurred with dinocap at 0·05% than at 0·025%, but the difference was usually reduced or nullified when captan was included. On James Grieve in 1956, dinocap at 0·05% without captan was more harmful than lime-sulphur.

As regards the effect of sprays on cropping (Table VII), varietal and seasonal differences are evident in a complex pattern of response. Cox's Orange Pippin yielded little information because of poor cropping, but in 1954 there was less crop

Table V.

Control of fruit tree red spider mite ; mean total number of mites and eggs on 32 sample leaves (4 trees).

Season	Month	Variety	Lime-sulphur	Dinocap with captan*		Dinocap without captan		Sig. diff. P=0·05
				0·05%	0·025%	0·05%	0·025%	
1954	July	C.O.P.	676 *2·83*†	52 *1·72*	115 *2·06*	46 *1·67*	100 *2·00*	*0·48*
	Aug.	C.O.P.	166 *2·22*	39 *1·59*	25 *1·40*	28 *1·46*	36 *1·56*	*0·50*
	Sept.	C.O.P.	27 *1·44*	20 *1·30*	10 *1·02*	9 *0·99*	22 *1·35*	*0·34*
	July	J.G.	645 *2·81*	46 *1·67*	65 *1·82*	54 *1·74*	95 *1·98*	*0·54*
	Aug.	J.G.	158 *2·20*	33 *1·52*	29 *1·47*	31 *1·49*	44 *1·65*	*0·48*
1955	Aug.	C.O.P.	280 *2·45*	200 *2·30*	316 *2·50*	80 *1·90*	256 *2·41*	*0·35*
		J.G.	416 *2·62*	158 *2·20*	355 *2·55*	148 *2·17*	181 *2·26*	*0·31*
		B.S.	1,148 *3·06*	269 *2·43*	724 *2·86*	295 *2·47*	525 *2·72*	*0·21*
		N.W.	616 *2·79*	245 *2·39*	549 *2·74*	165 *2·22*	417 *2·62*	*0·23*
1956	July	C.O.P.	550 *2·74*	59 *1·77*	137 *2·14*	42 *1·63*	199 *2·30*	*0·39*
	Aug.	C.O.P.	396 *2·60*	112 *2·05*	256 *2·41*	300 *2·48*	388 *2·59*	*0·41*
	July	J.G.	380 *2·58*	57 *1·76*	87 *1·94*	79 *1·90*	102 *2·01*	*0·39*

* 0·05% captan. † Data in italics transformed, see p. 20.

with lime-sulphur than with the dinocap treatments. The sulphur-shy Newton Wonder responded adversely to lime-sulphur in 1955 and 1956, and similarly to dinocap at 0·05% in 1955. James Grieve and Bramley's Seedling, however, cropped best with lime-sulphur and with dinocap at 0·025% ; at 0·05%, dinocap reduced the crop, although sometimes this effect was counteracted by the inclusion of captan.

TABLE VI.

Incidence of spray damage (fruit russeting) ; mean percentage or severity index of russet per tree.

Season	Variety	Russet	Lime-sulphur	Dinocap with captan*		Dinocap without captan		Sig. diff. P=0·05
				0·05%	0·025%	0·05%	0·025%	
1954	C.O.P.	%	71·5	23·1	34·7	41·8	25·5	
			57·7†	*28·7*	*36·1*	*40·3*	*30·3*	*9·1*
1955	C.O.P.	Severity index	140·4	64·2	41·6	76·4	40·6	37·1
	J.G.		96·6	66·1	61·0	77·6	55·1	15·1
	N.W.		19·2	5·5	7·0	16·3	7·4	10·1
1956	C.O.P.	%	62·3	41·2	28·3	49·3	40·0	
			52·1	*39·9*	*32·1*	*44·6*	*39·2*	*15·6*
	J.G.	%	13·1	16·0	7·2	34·1	9·8	
			21·2	*23·6*	*15·6*	*35·7*	*18·2*	*8·2*
		Severity index	15·1	16·5	7·3	36·5	10·8	10·3

* 0·05% captan. † Data in italics transformed, see p. 20.

DISCUSSION.

These data were derived from small, randomized plots of dwarf-pyramid trees which can be thoroughly sprayed because they are small and compact ; moreover, summer pruning itself helps to control the organisms under discussion. On the other hand the spray programme was deliberately limited to facilitate comparison of treatments. Both aspects must be taken into account in interpreting the results for commercial practice.

The sprays as fungicides.

The results have demonstrated no substantial and consistent difference between lime-sulphur and the dinocap/captan mixture for the control of scab and mildew. In spite of slightly better mildew control, there was clearly nothing to be gained economically by using dinocap at more than the normal field strength of 1 lb. of the 25% wettable powder per 100 gallons, especially when it was allied to half-strength captan. The presence or absence of the captan made no real difference to the effect of dinocap against foliage mildew in summer. Summer pruning is unlikely to have masked any differences, for these would already have been well established by July ; the pruning would merely limit the natural increase in existing differences.

The sprays as acaricides.

The trends shown by the data in Table V cannot be fully explained in the absence of detailed information on the predator status of the individual plots. In commercial practice, however, where much larger areas would be sprayed alike, the later progress towards red spider/predator equilibrium would probably be longer delayed in the absence of any reciprocal influence of neighbouring small plots.

Table VII.

Incidence of spray damage (loss of crop) ; mean number of fruits set and matured per 100 blossom trusses ; weight of fruit in lb. per tree.

Season	Variety	Crop	Lime-sulphur	Dinocap with captan*		Dinocap without captan		Sig. diff. P=0·05
				0·05%	0·025%	0·05%	0·025%	
1954	C.O.P.	Set	46·1	81·8	57·3	72·6	63·8	28·4
		Matured	24·1	43·1	34·3	42·6	36·9	
			29·4†	*41·0*	*35·8*	*40·7*	*37·4*	*6·8*
		Weight	5·7	9·9	8·6	9·7	8·9	1·8
	B.S.	Set	37·2	35·6	30·5	26·6	45·0	8·9
		Matured	34·4	33·1	27·3	25·1	42·7	
			35·2	*35·1*	*31·5*	*30·1*	*40·8*	*5·6*
		Weight	4·4	4·3	3·2	3·6	5·6	n.s.
1955	J.G.	Set	77·9	51·4	64·7	37·6	59·3	23·3
		Matured	27·3	21·8	26·0	19·2	28·5	7·1
		Weight	11·7	10·0	11·8	8·7	12·4	3·1
	B.S.	Set	20·8	11·3	11·8	7·8	13·5	5·2
		Matured	19·6	11·3	11·5	7·6	13·3	5·4
		Weight	4·2	2·0	3·0	1·9	3·3	1·7
	N.W.	Set	7·5	7·3	16·1	8·0	12·3	6·1
		Matured	7·4	7·2	15·9	7·9	11·8	6·1
		Weight	2·2	2·3	5·0	2·2	3·5	2·0
1956	J.G.	Set	35·2	29·1	26·4	20·8	35·8	n.s.
		Matured	19·0	16·5	20·2	13·4	18·3	5·2
		Weight	8·5	7·7	8·6	6·7	9·6	n.s.
	B.S.	Set	43·4	28·0	37·1	25·5	40·7	16·9
		Matured	37·2	25·2	34·4	22·8	36·2	n.s.
		Weight	11·3	5·0	9·1	4·9	7·8	5·8
	N.W.	Set	21·5	31·9	28·6	33·3	31·0	10·5
		Matured	13·8	25·5	22·6	28·7	24·1	8·4
		Weight	4·2	11·1	7·5	9·5	9·1	2·3

* 0·05% captan. † Data in italics transformed, see p. 20.

The various levels of red spider/predator control shown by each of the sprays would doubtless have been sustained longer with more post-blossom applications, though these would heighten the disparity in costs between the various programmes. Dinocap gave better red-spider control than lime-sulphur, which at 1% provides only a partly-lethal dose. Doubling the strength of dinocap produced a commensurate reduction in red-spider infestation, at least in the early stages, yet it must be regarded as doubtfully economic, especially in view of the increased risk of spray damage discussed below.

Although necessary for scab control, the inclusion of captan with dinocap was not always an advantage in controlling red spider.

Phytotoxicity.

To the above considerations must be added the evidence on spray damage, from which some clear trends are apparent. In comparison with the weaker

dinocap/captan mixture, lime-sulphur damaged the sulphur-shy Cox's Orange Pippin and Newton Wonder, but not Bramley's Seedling. James Grieve showed more fruit-russet from lime-sulphur in 1955 only.

Doubling the strength of dinocap increased the risk of fruit-russeting and loss of crop. Evidently some of the organic fungicides, like the inorganic ones, are safe and effective as high-volume sprays only within relatively narrow limits of concentration. There was clear evidence that captan could palliate these adverse side effects to some extent, but its use could scarcely be advocated merely to strengthen the case for increasing the concentration of dinocap.

Conclusions.

Where both apple scab and powdery mildew must be taken into account, the choice among the high-volume sprays in this experiment evidently lies between lime-sulphur and normal-strength dinocap plus captan—the latter at only half-strength to allow for some effect of the dinocap against scab, thus reducing costs.

On the lime-sulphur-shy varieties, Cox's Orange Pippin and Newton Wonder, the organic mixture is preferable to guard against spray damage and incidentally to take advantage of the better residual control of fruit tree red spider mite offered by dinocap. On varieties more tolerant of lime-sulphur, such as James Grieve and Bramley's Seedling, there is less reason to use the more costly mixture. The decision will evidently rest mainly on the relative value of the variety as a crop ; on the importance of the mite as a pest ; and on the merits attributed to dinocap in the absence of a more specific acaricide in the spray programme. Lime-sulphur at 1% may suffice to keep the mite under control while spraying is sustained.

SUMMARY.

In a comparison of high-volume sprays, continued at East Malling for three seasons on dwarf-pyramid trees, a mixture of dinocap (2:4-dinitro-6-(1-methyl-*n*-heptyl)phenyl crotonate) and half-strength captan was preferable to lime-sulphur for the varieties Cox's Orange Pippin and Newton Wonder as incurring less risk of spray damage, though providing no better control of scab and powdery mildew. On the varieties James Grieve and Bramley's Seedling, which are more tolerant of sulphur, the less costly inorganic spray compared more favourably, except that on all varieties it was inferior to dinocap in controlling the fruit tree red spider mite.

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PLUM ROOTSTOCK TRIALS AT EAST MALLING

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Investigations on rootstocks for plums began at East Malling over forty years ago. Hatton (1921, 1930; Hatton *et al.*, 1928-29) reported the botanical features of the rootstocks, their selection and propagation, and results of nursery trials. Tydeman (1957) gave botanical descriptions of rootstocks of commercial importance.

The early results of plum rootstock field trials at East Malling, up to 1934, were reported by Hatton (1936, 1939). The present paper covers the period from 1934 to 1956, and includes further data from some of the trials initiated by Hatton and also data from two more recent trials.

DESCRIPTION OF THE TRIALS.

Nine plum rootstock trials were planted at East Malling between 1922 and 1925 with one- or two-year-old trees. The trees in these trials were not arranged at random, but the results from different trials confirm each other and are supported by those from the later ones. The early trials were described by Hatton (1936).

Layout of trials ; rootstocks and varieties used.

The later trials, to be considered in this paper, were planned to allow statistical analysis of the results, and included many of the same scion varieties and rootstocks as the early ones.

Three trials were planted in 1928. *Trial A* comprised ten randomized blocks of Czar on Common Mussel, Myrobalan B, two clonal selections of Damas, and four of St. Julien. *Trial B*, also in ten randomized blocks, was of Cambridge Gage, Pershore and Victoria on Common Mussel, Common Plum, Myrobalan B and " own roots ". *Trial C* included seven randomized blocks of Cluster Damson on Common Mussel, Myrobalan B and " own roots ". *Trial D*, planted in 1938, included Victoria on twelve rootstocks—Aylesbury Prune, Common Plum, Myrobalan B, three selections of Damas, four of St. Julien and two of Kroosjespruim, in four randomized blocks ; and Czar on five rootstocks—Aylesbury Prune, Myrobalan B, one Damas and two St. Juliens, also in four randomized blocks.

The latest of the trials considered here, *Trial E*, was planted in 1941, and consisted of seven randomized blocks of Cambridge Gage, Denniston's Superb, Early Transparent and Oullins Golden Gage on three or more of the following rootstocks—Brompton, Brussels, Common Mussel, Common Plum, Marianna and Myrobalan B.

Notes on the rootstocks.

The long-established rootstocks, which have always been propagated vegetatively by layers or cuttings, or by taking suckers from fruiting plantations, include Brompton, Brussels, Common Plum, Marianna, the Mussels, and Pershore Yellow

Egg. Of the Mussels, only Common Mussel has been used in trials planted since 1926, and this is the only one that will be considered here. Brussels has been omitted since published work has shown it to have little value as a rootstock (Hatton, 1936, 1939 ; Hatton *et al.*, 1925 ; Swarbrick, 1936). Subsequent experience has confirmed this.

Aylesbury Prune, sometimes known as Michaelmas Prune, originally a local variety from Buckinghamshire grown on its own roots, is now sometimes used as a rootstock for other varieties.

Clonal selections have been made at East Malling from rootstocks that were traditionally propagated from seed. These selections have been propagated vegetatively by either layers or cuttings. Rootstocks in this group include selections of Myrobalan, St. Julien, Damas and Kroosjespruim. The characters on which the selections were made were described by Hatton (1921, 1936). Botanical descriptions of the shoots, leaves and fruits of the East Malling clonal selections of all the rootstocks reported on here have been given by Tydeman (1957).

Myrobalan selections.

Five clonal selections were used in early field trials, viz. Myrobalans A, B, C, D and E. All were very vigorous as rootstocks (Hatton, 1936), but only one, Myrobalan B, proved worthy of inclusion in further trials. It has been used in many subsequent trials and has become a standard against which other rootstocks can be judged.

St. Julien and Damas selections.

These two types have been used for many years, particularly on the Continent of Europe. In the past they were generally raised from seed, with some selection in the nursery to obtain seedlings of similar vigour.

Hatton (1936) pointed out that, although they were reputedly dwarfing rootstocks, they were far from uniform and that clonal selections covered a wide range of vigour as rootstocks.

Among the St. Juliens, selections were made from the range of types exhibited and six clones have been used in field trials at East Malling. St. Juliens A, B, C and D were used in early trials reported by Hatton (1936), and also in Trial A reported here. St. Juliens A, B and D, and two later clonal selections J and K were used in Trial D. St. Juliens B, C and D have now been discarded, as being no improvement on other more widely used rootstocks of similar vigour.

Three clonal selections of Black Damas, A, C and E, and one of White Damas, WD4, have been used in field trials. The only one that has been retained is Damas C, the others not having proved outstanding in any way.

Kroosjespruim selections.

Two selections, K3 and K5, were used in Trial D, but both induced only light crops in the scion and so have not been considered further.

" Own root " plums.

Many plums are grown locally on their own roots, e.g. Cambridge Gage and Pershore Yellow Egg. Eight such varieties have been included in trials at East Malling, both as " own root " trees, and occasionally also as rootstocks for other scion varieties. The results for four of these are described from Trials B and C.

Cambridge Gage, Pershore Yellow Egg and Warwickshire Drooper have been widely used in commerce, both to raise " own root " trees and as rootstocks for other varieties. They were often propagated from suckers. This led to admixtures of " rogues ", for seedlings must often have been mistaken for suckers in the orchards. It is generally recognized, for example, that there are many types in use under the name Pershore Yellow Egg. The clonal selection used as a rootstock at East Malling has been selected as typical of the variety in all recognizable characteristics (Tydeman, 1957).

Compatibility.

In plums both scion varieties and rootstocks include a wide range of types, and more than one species. The botanical classification of plum rootstocks is far from clear (Tydeman, 1957) ; however, botanical relationships seem to have little bearing on compatibility. For example, Czar " takes " badly on Brussels though both scion and stock show mainly *Prunus domestica* characters (Rehder, 1947), but it grows well on Myrobalan B (*P. cerasifera*).

Brompton and Pershore have mainly *P. domestica* characters, Common Mussel and Common Plum have characters of both *P. domestica* and *P. insititia*. The first three are compatible with all plum varieties that have been worked on them, as well as with damsons and peaches. Common Plum, on the other hand, is much less widely compatible and is unsuitable for Czar, Marjorie's Seedling, President, damsons, and for peaches.

Myrobalan B (*P. cerasifera*) has wide compatibility with plums and damsons. The only commercial varieties that are unreliable on it are Comte d'Althann's Gage and Oullins Golden Gage.

Marianna (*P. cerasifera* × *munsoniana*) is more limited in its compatibility and is not suitable for Czar, Denniston's Superb, Marjorie's Seedling, Oullins Golden Gage, damsons, and for peaches.

The three selections of St. Julien and the one of Damas reported on in this paper have proved compatible with all varieties of plums tested on them. St. Julien A and Damas C are also compatible with peaches.

Specimen trees.

Many plum rootstocks have been grown as trees on their own roots in the arboretum at East Malling, and show interesting differences in tree size and habit. Table I gives measurements of trunk cross-section, and height and spread of trees, at 18 years old. Some make very large trees, e.g. Myrobalan B and Aylesbury Prune ; others, e.g. Damas C and St. Julien J, make tall, narrow trees ; at the other extreme is Marianna which makes a round, low tree, almost bush-like in habit. It will be shown later that these differences are not necessarily reflected in the size and habit of a scion worked on them ; for example, Aylesbury Prune which is a large tree in the arboretum is semi-dwarfing as a rootstock.

Virus status.

In Trial E all trees of Cambridge Gage on Common Plum showed some symptoms of bark split virus, and a few of the Oullins Golden Gage on this rootstock also showed mild symptoms. Thus probably all the trees on Common Plum in this trial were

TABLE I.

Size of rootstock varieties, grown on their own roots, as arboretum trees 18 years old.

	Trunk cross-section (sq. cm.)	Height (m.)	Spread (m.)
Myrobalan B	586	9·0	7·9
Aylesbury Prune	482	7·8	8·0
Damas C	343	9·3	4·4
Marianna	342	6·0	7·9
St. Julien J*	338	8·7	6·6
Brompton	282	7·9	5·6
Common Plum	172	7·3	5·5
St. Julien A	184	5·6	5·5
Common Mussel	183	5·3	5·5
Pershore	143	6·3	5·1
St. Julien K	166	5·3	5·3

* St. Julien J one year younger.

infected with the virus, although not showing symptoms. However, there is no record of such symptoms on trees of Cambridge Gage on Common Plum in the earlier Trial B.

Apart from this no virus symptoms were observed in these rootstock trials.

GROWTH AND CROPPING OF TREES.

EARLIER NON-RANDOMIZED TRIALS.

Figures from trials planted between 1922 and 1925 were given by Hatton (1936, 1939), and later results from these same trials confirmed his earlier findings.

TABLE II.

Trunk cross-section (sq. cm.) and accumulated crops (lb.) per tree ; trees planted as two-year-olds in 1922, grubbed at 25 years old.

	Trunk cross-section (sq. cm.)		Accumulated crop (lb.)	
	at 15 years	at 25 years	at 15 years	at 25 years
VICTORIA on:				
Myrobalan B	219	394	454	1,607
Brompton	191	344	344	1,622
Marianna	127	197	530	1,691
Pershore	119	214	346	1,381
Common Plum	111	214	254	1,214
Common Mussel	109	206	247	1,204
RIVERS' EARLY PROLIFIC on:				
Myrobalan B	166	314	267	1,226
Marianna	148	250	264	1,107
Brompton	132	248	164	843
Common Mussel	106	223	170	936
Common Plum	110	201	181	887
Pershore	99	186	142	839

Table II gives results from two of these early trials and shows tree size as measured by trunk cross-section, together with accumulated crops for Victoria and Rivers' Early Prolific on six different rootstocks. These trees were planted in December 1922 as two-year-olds and were grubbed in 1945 at the age of 25 years. The figures show that the relative differences in tree size and cropping were the same at 15 years old as at 25. This appears to be generally true for plum rootstock trials at East Malling.

Plum trials are liable to reduction in number of trees, owing to disease, in later years ; it therefore seems appropriate to give all results on trees at 15 years old, even where the trials may have continued for some years after this.

Later randomized trials.

Vigour.

Tables III to VI give the size of tree, as measured by the area of cross-section of the trunk, for ten rootstocks under various scion varieties in Trials A to E. Standard errors are given as a percentage of each mean (Pearce, 1943).

Table III.

Trunk cross-section and accumulated crop per tree ; Trial A.

	Trunk cross-section (sq. cm.) at 15 years	Accumulated crop (lb.)	
		at 10 years	at 15 years
Czar on:			
Myrobalan B	131	72	541
Damas C	88	55	338
St. Julien A	75	47	304
Common Mussel	67	34	211
Standard error	*8·3%*	*5·5 lb.*	*35·5 lb.*

The largest trees, with all scions, were those on Myrobalan B, which is clearly a vigorous rootstock. Next come those on Brompton (Table VI) or St. Julien J (Table V). These are both semi-vigorous rootstocks. Common Mussel, Damas C and Marianna usually made trees smaller than those on Brompton, but not as small as those on Common Plum, although there were exceptions. Where Common Plum was included, the results confirmed earlier findings that it is a semi-dwarfing rootstock.

Figures from Trials A and D (Tables III and V) also confirmed earlier findings (Hatton, 1936) that St. Julien A is in the semi-dwarfing class of rootstocks, trees on it behaving very similarly to those on Common Plum. It has the added advantage that it is compatible with all varieties of plums, whereas Common Plum is unreliable with several.

Aylesbury Prune is also semi-dwarfing as a rootstock (Table V). St. Julien K, with both Victoria and Czar, made trees smaller than those on Common Plum, St. Julien A or Aylesbury Prune (Table V). It could therefore be classed as dwarfing.

It was originally considered that the maximum size of tree for any variety was obtained, by growing it on its own roots (Barker, 1928), but Hatton (1936) showed that it was possible to increase the tree size of a variety by grafting it on to

TABLE IV.

Trunk cross-section and accumulated crop per tree ; Trials B and C.

	Trunk cross-section (sq. cm.) at 15 years	Accumulated crop (lb.)	
		at 10 years	at 15 years
Trial B			
CAMBRIDGE GAGE on:			
Myrobalan B	439	37	435
Own roots	318	25	305
Common Mussel	232	26	209
Common Plum	191	18	184
Standard error	*6·4%*	*3·1 lb.*	*19·6 lb.*
VICTORIA on:			
Myrobalan B	175	49	425
Own roots	155	70	559
Common Mussel	92	48	258
Common Plum	88	34	243
Standard error	*5·8%*	*10·7 lb.*	*29·8 lb.*
PERSHORE YELLOW EGG on:			
Myrobalan B	207	97	756
Own roots	129	96	611
Common Mussel	115	61	388
Common Plum	76	53	294
Standard error	*5·9%*	*8·4 lb.*	*36·1 lb.*
Trial C			
CLUSTER DAMSON on:			
Myrobalan B	169	119	706
Common Mussel	111	79	387
Own roots	103	96	454
Standard error	*7·5%*	*13·2 lb.*	*55·3 lb.*

a vigorous rootstock. Later evidence has confirmed this and, of the six varieties grown on their own roots and reported on by Hatton (1936) as 12-year-old trees, all made trees similar in size to the same variety grafted on the intermediate Common Mussel, even at 23 years old.

Trials B and C included Cambridge Gage, Victoria, Pershore Yellow Egg and Cluster Damson on their own roots. Table IV shows that three of these four varieties on their own roots never became as large as when grown on Myrobalan B. The fourth variety, Victoria, behaved as if on a vigorous rootstock. It is the only variety grown as " own root " trees at East Malling which has proved considerably larger on its own roots than on Common Mussel. " Own root " Victoria trees were very nearly as large as Victoria on Myrobalan B (Table IV).

These results support those reported by Kasjjanenko (1950) who found that trees of Victoria were larger on their own roots than on Myrobalan seedlings, while the converse was true for Greengage and two other varieties (see also Johansson, 1957).

Tree shape, as measured by height and spread, was similar in " own root " trees to that of trees on other rootstocks of similar vigour.

TABLE V.

Trunk cross-section and accumulated crop per tree ; Trial D.

	Trunk cross-section (sq. cm.) at 15 years	Accumulated crop (lb.)	
		at 10 years	at 15 years
VICTORIA on:			
Myrobalan B	197	160	820
Damas C	164	110	618
Aylesbury Prune	125	110	583
Common Plum	124	106	588
St. Julien A	122	106	527
St. Julien K	111	136	667
*Standard error**	*7·0%*	*25·9 lb.*	*54·9 lb.*
CZAR on:			
Myrobalan B	162	55	774
St. Julien J	124	65	709
Aylesbury Prune	110	61	538
St. Julien K	95	66	599
*Standard error**	*11·4%*	*6·6 lb.*	*68·2 lb.*

* The standard errors quoted are for Myrobalan B under Victoria and for St. Julien K under Czar. For the other rootstocks the figures are rather less, as more trees survived.

TABLE VI.

Trunk cross-section and accumulated crop per tree ; Trial E.

	Trunk cross-section (sq. cm.) at 15 years	Accumulated crop (lb.)	
		at 7 years	at 15 years
CAMBRIDGE GAGE on:			
Myrobalan B	391	9	473
Common Mussel	291	4	337
Brompton	286	4	358
Marianna	195	8	268
Common Plum	138	7	196
Standard error	*8·9%*	*1·5 lb.*	*30·7 lb.*
DENNISTON'S SUPERB on:			
Myrobalan B	356	20	634
Brompton	233	5	411
Common Mussel	221	3	282
Common Plum	180	4	319
Standard error	*8·5%*	*1·7 lb.*	*44·6 lb.*
EARLY TRANSPARENT on:			
Myrobalan B	143	16	560
Brompton	102	4	432
Marianna	96	6	361
Standard error	*6·3%*	*1·3 lb.*	*26·5 lb.*
OULLINS GOLDEN GAGE on:			
Common Mussel	281	2	371
Brompton	262	0	373
Common Plum	171	5	377
Standard error	*4·1%*	*0·8 lb.*	*33·8 lb.*

Yield.

Tables III to VI also give the accumulated crop per tree for each trial. When these figures are compared with those for tree size it is clear that in general the larger trees carried the heavier crops.

Thus trees on Myrobalan B carried the heaviest crops, and those on the semi-dwarfing rootstocks the lightest. The rootstock effect on cropping appeared to be an indirect one, the rootstock governing the tree size, which in turn determined the amount of crop. This confirms earlier observations (Swarbrick, 1936). There were some exceptions ; for example, Oullins Golden Gage on Common Plum, and Victoria and Czar on St. Julien K, carried heavier crops than would have been expected from the size of tree (Tables V and VI). Conversely, trees on Common Mussel sometimes cropped less than would have been expected from the size of tree (Trial C, Table IV, and under Denniston's Superb, Table VI).

Pershore Yellow Egg and Victoria on their own roots cropped more heavily than the same size tree on Common Mussel and Myrobalan B respectively.

Where tree spreads have been recorded, suitable planting distances can be estimated for each rootstock-scion combination. Estimated yields per acre, based on the actual yields at uniform spacing and adjusted to the spacings shown, are given in Table VII for Trials B and E. The estimated figures show that, where

TABLE VII.

Estimated accumulated crops at 15 years old, in tons per acre, at appropriate spacings ; Trials B and E.

Variety	Rootstock									
	Myrobalan B		Brompton		Common Mussel		Marianna		Common Plum	
	Spacing (ft.)	Crop (tons)	Spacing (ft.)	Crop (tons)	Spacing (ft.)	Crop (tons)	Spacing (ft.)	Crop (tons)	Spacing (ft.)	Crop (tons)
Trial B										
CAMBRIDGE GAGE	22	17½			18	12½			17	12
Trial E										
CAMBRIDGE GAGE	22	19	20	17	20	16	18	16		
DENNISTON'S SUPERB ..	22	25	20	19	20	13½			18	19
EARLY TRANSPARENT ..	16	42	15	37½			15	31		
OULLINS GOLDEN GAGE			20	18	20	18			18	22½

Myrobalan B was included, trees on this rootstock gave the heaviest crops per acre in spite of the wider planting distances necessary.

Fruit size.

Evidence for an effect of rootstock on fruit size is inconclusive. Records of the mean weight of fifty fruits were very variable, but indicate that rootstocks which induced heavy crops did not produce smaller fruits.

Earliness of ripening.

With some varieties all the fruit is picked at the same time, and this is done with nearly all varieties in years of light crops. With other varieties, particularly early ones, the ripest fruit is picked first, the rest being cleared later. In such cases the proportion of the crop harvested at the first picking gives an indication of the earliness of ripening of the fruit.

TABLE VIII.

Percentage of fruit in first picking ; Trials A, B and E.

Variety	Rootstock			
	Myrobalan B	Brompton	Common Mussel	Common Plum
Trial A				
CZAR	19		27	
Trial B				
CAMBRIDGE GAGE	19		22	20
PERSHORE	25		40	36
VICTORIA	8		21	17
Trial E				
OULLINS GOLDEN GAGE ..		67	53	73

Table VIII gives the mean percentage of the crop in the first picking. The annual and tree-to-tree variations were large ; nevertheless the figures show that trees on Myrobalan B ripened their fruit later than those on Common Mussel or Common Plum. This difference in time of ripening was never more than three days.

Precocity in bearing.

In plums there is little evidence that precocity is correlated with a dwarfing habit. Trees on Myrobalan B, the most vigorous of the rootstocks considered here, were often the most precocious yielders, as illustrated in Trial E (Table VI). Earlier trials had shown that crops from trees on this rootstock were occasionally exceeded by those on Marianna or Pershore in the early years (Hatton, 1936).

Disease resistance.

Hatton (1936) showed clearly that varietal differences occur in the incidence of silver leaf (*Stereum purpureum*) and of bacterial canker (*Pseudomonas mors-prunorum*), but little difference was shown between trees of the same variety on different rootstocks.

Of the eight scion varieties included in these five trials, Victoria was the most susceptible to silver leaf. Most of the infected trees continued to show symptoms of silver leaf every year, or intermittently, but some showed symptoms for a year or two only. There was no evidence of more recovery from silver leaf in trees on one rootstock than on another.

With Victoria there was a tendency for trees on Common Mussel and Common Plum to have less silver leaf than those on Myrobalan B (Table IX). This was

probably not a direct effect of rootstock upon the resistance of the scion. The heavier cropping on Myrobalan B than on the other two rootstocks may have led to more branch breakages due to weight of crop, thus providing more chances of entry for the fungus, which is a wound parasite.

TABLE IX.

Percentage of trees with silver leaf ; Trial B.

Variety	Rootstock		
	Myrobalan B	Common Mussel	Common Plum
CAMBRIDGE GAGE	40	40	10
VICTORIA	71	57	50
PERSHORE	56	20	40

Although all the trees in these trials were low worked, there were not enough recorded cases of bacterial canker to show any differences between trees on the different rootstocks.

There was no evidence to suggest that trees on their own roots were healthier or less healthy than trees on different rootstocks.

DISCUSSION.

Differences in tree size due to rootstock effect are less striking in plums than in apples. Moreover, the scion variety has a large effect on tree size and on the size range between trees on different rootstocks (Hatton, 1936). With Cambridge Gage there was a large difference in size between trees on vigorous and dwarfing rootstocks, whereas this difference was small with trees of Early Transparent.

Differences between trees on different rootstocks increased as the trees aged, but the relative differences shown at fifteen years of age were similar to those at the end of trials which lasted more than fifteen years. This agrees with results from apple rootstock trials (Preston, 1959). It seems therefore that 15 years is adequate for plum rootstock trials.

The final size of tree is the result of the combined effect of the vigour of the roots and branches. This applies not only to a rootstock/scion combination, but also to possible differences in inherent vigour between the roots and branches of unworked trees (Vyvyan, 1955 ; Maggs, 1957). Thus, in the trials described here, Cambridge Gage made a large tree on all rootstocks, but a larger one on a vigorous rootstock such as Myrobalan B than on its own roots. It is vigorous as a scion, but only of intermediate vigour as a rootstock. Victoria, which made a medium-to-small tree on all rootstocks, was just as large on its own roots as on Myrobalan B. It is of intermediate vigour as a scion, but probably vigorous as a rootstock. Aylesbury Prune made a large tree in the arboretum on its own roots, but under Victoria and Czar it was a semi-dwarfing rootstock. However, it appears that, in general, the vigour of a variety on its own roots is an indication of its vigour as a rootstock under other scion varieties.

Nearly all the rootstocks used in these trials induced cropping in the scion proportional to the size of tree. Generally, trees on all rootstocks came into cropping at the same age, whether the rootstocks were vigorous or dwarfing. There is some evidence that trees on Marianna and Pershore cropped at an earlier age than on other rootstocks, and in Trial E trees on Myrobalan B cropped twice as heavily as trees on other rootstocks up to seven years of age.

Plums on their own roots were neither healthier nor more prolific than on rootstocks of similar vigour and cropping potentiality. Moreover, raising " own-root " trees from suckers is not satisfactory because of the risk of chance seedlings, and of spreading virus disease.

Of the many plum rootstocks, both established varieties and clonal selections from seedlings, that have been tested in field trials at East Malling, a large number were discarded for various reasons. A few have proved to be outstanding and worthy of recommendation, and it is possible to group these according to their effect upon the vigour of the scion.

For large high-yielding trees Myrobalan B has proved to be the most suitable rootstock, and it is compatible with all commercial plum varieties with the exception of Oullins Golden Gage. For slightly less vigorous trees, but also carrying slightly smaller crops, Brompton is the most suitable rootstock.

Among the rootstocks of intermediate vigour, trials reported by Hatton (1936) and in this paper have shown Marianna and Pershore to produce trees which crop heavily for their size. Pershore has been difficult to obtain true to type, but it is now available as clonal material and is a very useful rootstock, with its wide compatibility with all plum varieties.

For smaller trees, St. Julien A, with its wide compatibility, may well replace Common Plum as the most widely used rootstock, and for even smaller trees St. Julien K can be recommended.

SUMMARY.

1. Results are considered from five field trials of plum rootstocks, including both established rootstocks and clonal selections from seedlings.

2. Most plum rootstocks induced cropping in the scion proportional to the size of tree.

3. It is suggested that plum rootstock trials can be completed by the fifteenth year, as relative results remained unchanged thereafter.

4. There appears to be no advantage in growing plums on their own roots rather than on rootstocks of similar vigour and cropping potentiality.

5. The vigour of a variety grown on its own roots is not necessarily indicative of its vigour as a rootstock.

6. As a result of the trials discussed in this paper and earlier reports, the following rootstocks can be recommended:

Vigorous:	Myrobalan B
Semi-vigorous:	Brompton
Intermediate:	Marianna, Pershore
Semi-dwarfing:	Common Plum, St. Julien A
Dwarfing:	St. Julien K.

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ROOTSTOCK-SCION INTERACTION IN APPLES WITH SPECIAL REFERENCE TO ROOT ANATOMY

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Hatton (1935) established the general dominance of clonal rootstocks in determining tree vigour and cropping. There is also evidence that scion influence, though secondary, may sometimes be important (Roberts, 1949 ; Vyvyan, 1938 and 1954). A preliminary study of roots from a limited number of three-year-old trees (McKenzie, 1956) indicated that both rootstock and scion could be expected to influence root anatomy. The present observations were made to examine the relationship between scion vigour and root anatomy in four-year-old apple trees.

Material and methods.

Roots were taken from four-year-old apple trees which formed part of the root-stock-scion interaction trial described by Vyvyan aud Maggs (1954). For this trial, all sixteen combinations of M.IX, M.IV, M.II, and M.XVI had been budded in 1950, these clonal selections being used both as rootstocks and as scions. Un-worked rootstocks were also included and were cut back to a 4-inch snag in March 1951 at the time the budded trees were snagged back. On these unworked trees a bud in a corresponding position to that of the inserted " bud " on the worked trees was allowed to grow out (Maggs, 1954).

Three of the selections have been classified as follows : M.XVI, very vigorous ; M.II, vigorous ; M.IX, dwarfing (Hatton, 1935). The fourth selection, M.IV, was placed by Hatton among the semi-dwarfing rootstocks though the later experiments of Preston (1958) have shown that M.IV is considerably more vigorous than the semi-dwarfing M.VII, and it is now classified as of moderate vigour.

Ten trees of each rootstock-scion combination were lifted and two pieces of root measuring 10 mm. in diameter were taken from each tree, i.e. twenty roots of standard diameter were collected from each treatment. Transverse sections from each root were stained with safranin and aniline blue, mounted in Canada balsam, and recorded in the following ways :

Bark percentage, determined upon projected images (×10) by the method of Beakbane and Thompson (1947).

Wood-ray percentage, determined upon projected images (×100), the number and width of rays on four standard arcs located in the xylem being recorded on paper ribbon and the measurements used to calculate wood ray percentage. The arcs were situated at a distance of 200 microns from the cambium and each represented about $\frac{1}{16}$ of the perimeter. This linear method of recording was more rapid than the photomicrographic technique of Beakbane and Renwick (1936) and appeared to be equally accurate.

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Vessel areas, determined upon projected images (×300) of four fields located in the xylem in the same positions as those for the wood-ray measurements. A representative sample of ten vessels was selected in each field and the longest and shortest diameters of each vessel measured.

RESULTS.

Self-budded trees, i.e. M.IX/M.IX, M.IV/M.IV, M.II/M.II, and M.XVI/M.XVI, were regarded as standards for comparisons in evaluating the results, and data from these trees are shown in heavy type in the Tables. Data from unworked rootstocks have been omitted in calculating rootstock means, but they have been included for comparison in the general analyses of variance.

Bark percentage.

Bark percentage (Table I) is here defined as the percentage of bark in the total cross-sectional area of the root. There were large differences in root-bark percentages between the four self-budded rootstocks. The value for the dwarfing rootstock M.IX was twice that of the very vigorous rootstock M.XVI ; in fact, the proportions

TABLE I.

Bark percentage of roots of standard diameter (0·9-1·0 cm.) from each stock-scion combination and from unworked rootstocks.

Rootstock	Scion					Means of worked rootstocks
	Unworked	IX	IV	II	XVI	
IX	63·5	**63·9**	60·9	64·4	62·2	63·0
IV	45·2	51·6	**46·0**	43·6	47·1	46·7
II	39·6	48·8	41·8	**40·2**	43·3	42·7
XVI	29·1	35·0	31·8	28·7	**30·5**	31·0
Means of scions ..	44·3	49·8	45·1	44·2	45·8	

Significant difference:	P <0·05	P <0·01	P <0·001
between means of worked rootstocks ..	1·1	1·4	1·8
between means of scions	1·1	1·4	1·8
between stock-scion combinations (including unworked rootstocks) ..	2·2	2·8	3·7

of bark in the four rootstocks varied inversely with their potential vigour as classified by Hatton. Dwarfing clones used as scions increased the proportion of root-bark tissue in vigorous rootstocks ; thus the proportion of bark tissue in M.II, M.IV and M.XVI roots was approximately 5 to 8% greater under M.IX scions than in comparable self-budded trees. Vigorous scions, however, did not appreciably affect the proportion of bark tissue in dwarfing rootstocks. In the combination M.IV on M.IX the proportion of root-bark tissue in the M.IX rootstocks was approximately 3% less than in self-budded M.IX rootstocks.

Wood ray percentage.

There were large differences in wood-ray percentages between M.IX, M.IV and M.XVI (Table II). The dwarfing rootstock M.IX had 2½ times as much wood-ray tissue as the vigorous rootstock M.XVI. Self-budded trees of M.II and M.XVI had similar amounts of wood-ray tissue in their roots. Dwarf scions increased the proportion of ray tissue in vigorous rootstocks, e.g. under M.IX scions the wood-ray percentages of M.II and M.XVI roots increased by 5 to 10%. Vigorous scions reduced the proportion of wood-ray tissue in dwarfing rootstocks, e.g. the ray tissue of M.IX roots under M.IV and M.XVI scions was less, by 5 to 9%, than in M.IX roots from self-budded trees.

TABLE II.

Area of rays (% cross section) in xylem of roots of standard diameter from each stock-scion combination and from unworked rootstocks.

Rootstock	Scion					Means of worked rootstocks
	Unworked	IX	IV	II	XVI	
IX	38·6	**43·6**	38·8	42·8	34·9	40·0
IV	25·7	28·1	**26·1**	23·5	22·5	25·1
II	17·8	27·3	17·2	**17·8**	18·3	20·2
XVI	14·6	21·7	20·7	16·7	**17·0**	19·0
Means of scions ..	24·2	30·2	25·7	25·2	23·2	

Significant difference:	P <0·05	P <0·01	P <0·001
between means of worked rootstocks ..	1·0	1·3	1·6
between means of scions	1·0	1·3	1·6
between stock-scion combinations (including unworked rootstocks) ..	1·9	2·5	3·2

Roots of self-budded M.IX rootstocks had 5% more wood-ray tissue than those of unworked M.IX rootstocks, indicating an alteration due to the presence of a bud union. Similar differences between unworked and self-budded trees were shown by Maggs (1955) to exist in another character, viz. number of inflorescences per tree. Part, at least, of the apparent dwarfing effect of self-budding may have been in the nature of a delay rather than of a permanent restriction in growth. The bud which was allowed to grow on the unworked trees would already possess adequate vascular connections with the stem bearing it, whereas the inserted bud would not have been fully joined to the rootstock's vascular tissues at the commencement of growth, with resulting impeded flow of water and nutrients in the xylem, and of assimilates in the phloem, during the first phase of growth in the spring. The effect on anatomy of this restriction of growth apparently persisted for several years.

Data on number, width, and relative area of ray given by McKenzie (1956) showed that the influence of M.IX scions was on the frequency rather than on the size of the rays.

Vessel size.

There were large differences between the roots of self-worked M.IX, M.IV, M.II and M.XVI in mean vessel size, M.IX having the smallest and M.IV the largest vessels (Table III). Vessels in roots of unworked M.II rootstocks were nearly twice the size of those in roots of comparable self-budded trees. The unworked trees of

TABLE III.

Vessel size (sq. μ) in roots of standard diameter from each stock-scion combination and from unworked rootstocks.

Rootstock	Scion					Means of worked rootstocks
	Unworked	IX	IV	II	XVI	
IX	328	**589**	596	604	674	616
IV	2,015	682	**2,090**	890	899	1,140
II	1,155	780	691	**798**	727	749
XVI	651	994	742	637	**998**	843
Means of scions ..	1,035	761	1,030	732	825	

Significant difference:	P <0·05	P <0·01	P <0·001
between means of worked rootstocks ..	95	126	162
between means of scions	95	126	162
between stock-scion combinations (including unworked rootstocks) ..	190	251	323

this rootstock obviously differed greatly from the worked trees as shown also by Maggs (1955) for average number of inflorescences per tree. The smaller vessel size would be in line with the greater precocity of the trees in flowering. There was no consistent relationship between potential vigour of the scions and their influence on vessel size of rootstocks. The very large vessels of M.IV roots were, however, reduced in size to a remarkable degree by scions of M.IX, M.II and M.XVI.

TABLE IV.

Dry weight of stem (gm.) of each stock-scion combination and of unworked rootstocks (1954).

Rootstock	Scion					Means of worked rootstocks
	Unworked	IX	IV	II	XVI	
IX	288	**228**	436	367	619	412
IV	1,259	606	**928**	1,038	936	944
II	1,853	1,102	1,262	**1,653**	1,823	1,460
XVI	1,093	773	1,026	1,177	**1,049**	1,006
Means of scions ..	1,124	677	913	1,126	1,107	

Significant difference:	P <0·05	P <0·01	P <0·001
between means of worked rootstocks ..	183	243	312
between means of scions	183	243	312
between stock-scion combinations (including unworked rootstocks) ..	367	486	625

Growth rate and root anatomy.

It has been shown that various histological features of roots can be correlated with potential vigour of the clones used. This suggested that there might be a similar correlation between root structure and the actual growth rates of young trees. Data on dry weight of scion, supplied by Maggs, provide a sound measure of tree size at the age of four years (Table IV). Apples require several years to reach maturity and four years is too short a period for assaying the ultimate growth of the various clones, especially the more vigorous ones. However, the dwarfing influence of both the M.IX rootstocks *and* the M.IX scions was apparent at this age and this was consistently associated with a high proportion of bark tissue and wood ray tissue in the roots (Tables I and II).

TABLE V.

*Average number of inflorescences per tree (1954).**

Rootstock	Scion					Means of worked rootstocks
	Unworked	IX	IV	II	XVI	
IX	53·0	**43·1**	49·8	15·8	6·8	28·9
IV	1·7	27·5	**2·9**	0·2	0	7·7
II	1·8	80·8	13·4	**4·9**	0	25·0
XVI	0	3·6	0	0	**0**	0·9
Means of scions ..	14·1	38·8	16·5	5·2	1·7	

* Data quoted from Maggs (1955).

Influence of deblossoming on root structure.

Although the trees were only four years old at the time of sampling, some of them, especially those containing M.IX as rootstock or scion, had produced blossom for two seasons (Maggs, 1955). The number of inflorescences per tree is given in Table V. In treatments which produced blossoms, half the trees were deblossomed. The root structure of deblossomed trees was compared with that of blossoming trees (Table VI). It was apparent that both bark percentage and wood-ray percentage were less in roots of deblossomed trees than in those allowed to blossom and set fruit, whereas the vessels were larger.

TABLE VI.

Influence of deblossoming on root structure.

	Deblossomed	Not deblossomed	Level of significance
Bark percentage	55·8	57·0	$P < 0.05$
Wood-ray percentage ..	32·6	36·2	$P < 0.001$
Vessel size (sq. μ) ..	742	729	$P < 0.05$

DISCUSSION.

Rootstock vigour and root structure.

The present work has confirmed that, in general, the most vigorous rootstocks have the least bark and wood-ray tissue in their roots and, conversely, that the least vigorous rootstocks have the most. Where these rootstocks are worked with scions of greater or lesser vigour, some modifications in structure towards that of the scion are found, but these are not very great and the inherent structure of the clonal root appears, as reported by Beakbane (1953), to be relatively stable.

Rootstock-scion interaction.

Bark percentage in self-budded rootstocks ranged from approximately 30% of cross-sectional area for M.XVI roots to approximately 60% for M.IX roots. The small but significant modifications in bark tissue development that could be attributed to scion influence did not exceed an increase of 8% for dwarfing scions on vigorous rootstocks, and a decrease of 2% for vigorous scions on dwarfing rootstocks, thus indicating that the modifying influence of these scions on the inherent structure of the rootstocks is small in comparison with the differences between rootstock clones.

The proportion of ray tissue in wood of self-budded selections ranged from approximately 20% for M.XVI roots to approximately 40% for M.IX roots. Scion influence on proportion of ray tissue in wood of roots brought about modifications as great as 10%. Dwarf scions increased the ray tissue in the wood of M.XVI roots and vigorous scions decreased ray tissue in M.IX roots to a similar degree. It would seem that scion influence on root anatomy had relatively greater effect upon the proportion of wood-ray tissue than upon bark tissue development. Thompson (1952) demonstrated that dwarfing scions increased the amount of total living tissue in roots of a very vigorous rootstock. Results of this experiment confirm these conclusions and also indicate that the converse is true, viz. that vigorous scions decrease the amount of living tissue in roots of a dwarfing rootstock.

The large vessels of Malling IV.

In general, the size of vessels in wood of apple roots is directly correlated with tree vigour. In the present experiment by far the largest vessels were found in roots of the semi-vigorous rootstock, M.IV. This selection is unusual in that it combines histological features usually associated with strong growth, viz. large vessels, with other features generally related to the dwarf habit, viz. large amounts of bark and wood-ray tissue. To some extent this is reflected in its orchard performance. Malling IV is known to induce vigorous growth for several years after planting, followed by a period of intense cropping and limited growth. The vessels in the roots of self-budded M.IX, M.II, and M.XVI showed a trend towards a positive correlation between vessel size and tree vigour, but all were much smaller than the vessels in the roots of self-budded M.IV. It is significant that all three selections used as scions had the effect of greatly reducing vessel size in M.IV roots but the influence of M.IV as a scion did not increase the vessel size in the roots of M.IX, M.II, and M.XVI.

Blossoming and root anatomy.

In many plants, flowering and fruiting is associated with a reduced rate of vegetative growth. While Maggs (1955) showed that deblossoming was followed,

in young apple trees, by an increase in rate of shoot growth, Rogers (1939) noted that root growth in mature apple trees increased after spring frost damage to the blossom. Xylem production in apple stems has also been shown by Finch (1935) to be reduced as a result of blossoming, and a similar association between width of growth rings and fruiting was noted by Auchter and Schrader (1923) and Ljones and Nesdal (1954). Thus the effect of the presence of flowers or fruits on the growth rate of apple shoots and roots has been clearly established but the influence of flowering on root structure had not previously been studied. In the young trees of this present experiment, flowering has been shown to increase bark and wood-ray tissue in roots.

Reference to Tables IV and V shows clearly that trees containing M.IX as rootstock or scion were smaller and flowered more heavily than any of the others. From Tables I, II, and V it can be concluded that part of the influence of M.IX scions on root structure is associated with the presence or absence of flowers or fruits.

This work with four-year-old trees has shown that restriction of growth, either by the use of dwarfing rootstocks and scions or by the influence of flowers and fruit, is usually associated with some modifications in root structure—such as, for example, increase in proportion of bark tissue, enlargement of wood-ray tissue—and sometimes with diminution of vessel size. It is clear, however, that in such young trees the relation between growth rate and root structure is not simple and that additional studies on roots from a similar series of older trees, which would then show greater differences in size, would be desirable.

SUMMARY.

1. Bark percentages, wood-ray percentages and vessel sizes were determined on roots from four-year-old apple trees of a rootstock-scion interaction trial. This trial contained unworked rootstocks and all sixteen possible combinations of M.IX, M.IV, M.II and M.XVI, used both as rootstocks and as scions.

2. Root structure of unworked Malling rootstocks was constant and could be correlated with the potential vigour of the selections.

3. When stocks and scions representing extremes of vigour were combined, some modifications of the inherent root structure of the clonal rootstocks were apparent and these could be attributed to scion influence. In general the differences were not, however, as great as those between unworked or self-budded rootstock clones.

4. Restriction of tree growth, either by the use of dwarfing scion or rootstock or by natural flowering and fruiting, was associated with increased proportion of bark tissue in roots, enlargement of wood-ray tissue, and sometimes with diminution of vessel size.

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THE PRODUCTION AND MAINTENANCE OF VIRUS-FREE RASPBERRY PLANTS

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INFECTION by viruses is a major cause of poor growth and yield of raspberry plants. The viruses concerned are of two main kinds, those which are spread through the soil and those spread by aphids, chiefly by the common raspberry aphid, *Amphorophora rubi*. Outbreaks of severe diseases may occur whenever susceptible varieties of raspberry are planted on land which contains soil-borne viruses and no satisfactory means of control has yet been devised. Soil-borne viruses are, however, patchily distributed and their effects on susceptible raspberry varieties are usually so drastic that canes dug from diseased plants are unlikely to survive and thereby to act as sources of infection in new plantations. By contrast, the effects of infection by aphid-borne viruses are cumulative : infection by one such virus does not protect plants from infection by other similar viruses and vigour and yield decline with accumulating infections. Once infected, plants never recover and all canes dug from diseased plants are themselves diseased. Although, in Scotland at least, aphid-borne viruses spread only slowly, commercial raspberry stocks often deteriorate rapidly because the traditional use of planting material taken from fruiting plantations is a certain way of introducing sources of infection into new plantations. Because the symptoms caused by aphid-borne viruses are often inconspicuous, canes are usually taken indiscriminately from healthy and diseased plants. Thus, even slow spread of virus from many sources within a crop soon leads to total infection. There is little doubt that most infection spreads from sources within crops and, as both control of aphids and the roguing of infected plants in fruiting plantations are impracticable, the use of healthy planting stock is an obvious precaution.

Until recently, no virus-free plants of any raspberry variety were known. The best planting material available was derived either from stocks freed from severe disease by roguing, or from plants found, by graft-testing to suitable indicator plants, to contain only apparently innocuous viruses. Plants and pieces of root of Malling Jewel and Lloyd George raspberry were not freed from aphid-borne viruses when immersed for varying periods in water at temperatures of 35° C. to 50° C. (Cadman, unpublished) but, when potted plants of these varieties were kept for a week or more at an air temperature of 32° C., some of the survivors were virus-free (Chambers, 1954). In the first part of this paper the results of subsequent work are reported. These show that raspberry plants exposed to high temperature were freed from infection by some, but not by all, aphid-borne raspberry viruses. In the second part, the technique used to propagate virus-free material is described.

Materials and methods.

The incubators used were boxes, 3 ft. × 3 ft. × 3 ft., consisting of asbestos sheets bolted to an aluminium-alloy framework. Heat was supplied by a set of ten 120-w. electric tubular heaters fixed to the floor, and controlled by a stem-type

thermostat fitted in the roof of each box. Racks, 18 in. from the floor, supported metal boxes containing potted plants packed in damp peat, and a 400-w. mercury vapour lamp, fitted over a hole cut in the roof panel, supplied light for 17 hours daily. This hole was covered with a sheet of heat-resistant glass which cut off most of the radiant heat from the mercury vapour lamp. The level of humidity in the boxes was uncontrolled but the potted plants and the peat in the trays were kept damp by regular watering. The asbestos panels were fitted sufficiently loosely to allow a good circulation of air through the boxes. Electrically-operated fans were not used because it was found that plants exposed to a rapid circulation of warm air suffered severely from leaf scorching. The boxes were kept in a dark room where the ambient air temperature varied little. Under these conditions the air temperature in the boxes varied within only $\pm 0{\cdot}5°$ C. of the desired level.

Preliminary trials showed that raspberry plants usually died if exposed to high temperature too soon after they were potted. Plants were therefore allowed to become well established by growing them in pots or boxes kept outdoors for one season before treatment. Most tests were made in late winter with dormant plants which had been potted up the previous spring, but the time of treatment seemed immaterial provided the plants were well established. Treated plants were transferred to a heated glasshouse and tested for virus by grafting shoots from them to plants of *Rubus henryi* (Cadman, 1951). Those which seemed free from virus when first tested were re-tested several months later.

Tests were made with plants of Norfolk Giant containing raspberry leaf mottle virus (Cadman, 1951), of Malling Jewel containing a mixture of viruses including raspberry leaf spot virus (Cadman, 1952d), and with plants of Malling Promise, Lloyd George (New Zealand stock) and other varieties and seedlings containing unidentified latent viruses. One experiment was also made with Norfolk Giant plants infected with vein chlorosis, vein-banding, or yellows diseases (Cadman, 1952a, 1952b, 1952c).

EXPERIMENTAL RESULTS.

Heat therapy of virus-infected raspberry plants.

The results in Table I show that plants of Malling Jewel and Norfolk Giant were freed from infection by latent viruses after only 6-10 days' (actually 7 and 8 respectively) exposure at 32° C. Although there was a general tendency for the numbers of plants cured to increase with increasing length of exposure, the results of individual experiments varied erratically. Too few tests were made to show whether treatment at 35° C. was more effective than at 32° C. A higher proportion of Malling Jewel and Norfolk Giant plants were cured than of Lloyd George and Malling Promise, but this result is difficult to interpret. Differences in varietal reaction cannot be discounted. On the other hand, there is evidence that the plants of Lloyd George and Malling Promise used in the trials contained viruses different from those present in the Norfolk Giant and Malling Jewel plants (Cadman, unpublished) and the results may indicate differences between these viruses in their ability to survive in plants at high temperature.

Evidence that aphid-borne raspberry viruses differ in their response to temperature was provided by tests made with Norfolk Giant plants infected with either vein-banding, vein chlorosis, or yellows diseases. In one of several experiments,

TABLE I.

The results of exposing virus-infected raspberry plants to high air temperature.

No. of days exposed	Temperature ° C.	Norfolk Giant			Malling Jewel			Lloyd George			Malling Promise		
		No. treated	No. surviving	No. virus-free	No. treated	No. surviving	No. virus-free	No. treated	No. surviving	No. virus-free	No. treated	No. surviving	No. virus-free
5	32	4	3	0	—	—	—	4	3	0	—	—	—
6-10	32	12	9	3	14	14	3	4	3	0	8	8	0
	35	4	4	0	4	4	0	4	4	0	4	4	0
11-15	32	8	4	2	10	8	7	4	2	0	4	4	0
	35	4	4	0	4	4	0	4	4	0	4	4	0
16-20	32	8	8	2	8	8	2	—	—	—	8	8	3
	35	8	8	2	8	8	0	8	8	1	8	8	1
21-35	32	—	—	—	6	2	2	8	1	1	—	—	—
Total		48	40	9	54	48	14	36	25	2	36	36	4
% plants virus-free			22·5			29·1			8·0			11·1	

diseased plants were exposed for 60 days at 40° C. Although most were freed from leaf mottle virus, none was freed from the viruses which cause the leaf symptoms characteristic of the other diseases. At first the plants produced shoots without symptoms but within a few weeks all the new growth displayed characteristic symptoms of systemic infection. With the exception of vein chlorosis disease, which is transmitted by *Aphis idaei* (Cadman, 1952a) and about which little else is known, most aphid-borne raspberry viruses are transmitted by *Amphorophora rubi* and all seem to be viruses that persist for short periods in the vector (Cadman, 1954 ; Stace-Smith, 1956). The ability of the " mosaic " components of vein-banding, vein chlorosis and yellows diseases to survive in plants in which leaf mottle virus has been inactivated by treatment for long periods at high temperature is the first evidence that aphid-borne raspberry viruses differ in this respect.

Cuttings made from young, rapidly growing shoots of virus-infected plants, or from shoots produced by infected plants during a period of heat treatment, are sometimes free from viruses even though the parent plants may still be infected (Holmes, 1948 ; Kassanis, 1954 ; Hollings and Kassanis, 1957). This also occurs with the raspberry.

In January 1956 root cuttings taken from a cane nursery of Malling Jewel were planted in boxes, six of which were placed in the incubator at 35° C. and six in a heated glasshouse. Young shoots were cut off as soon as they appeared and rooted in a propagating case by the method described by Hudson (1954) and Williams and Hudson (1956). The plants were grown on and tested for virus infection by grafting to plants of *R. henryi*. The results (Table II) show that nearly all plants produced from root cuttings grown at glasshouse temperature (around 20° C.) were virus-infected, whereas at least half of those produced from root cuttings which had been kept at 35° C. were not.

TABLE II.

Proportion of virus-free plants produced from roots of Malling Jewel raspberry grown at different temperatures.

Temperature (° C.)	Number of days exposed				Total
	7	10	16	21	
37	2/7*	0/2	4/5	2/2	8/16
20	1/5	1/4	0/5	0/3	2/17

* Number of plants virus-free to number of cuttings rooted.

Heat treatment is a relatively simple means of obtaining virus-free raspberry plants, but it has the limitation that only certain viruses can be eliminated. Furthermore, prolonging the exposure to high temperature does not necessarily effect a higher proportion of cures, and all surviving plants need careful and repeated testing before any can be assumed to be free from virus.

In the course of this work virus-free plants of the following varieties were obtained : Burnetholm Seedling, Lloyd George, Malling Enterprise, Malling Jewel, Malling Landmark, Malling Promise and Norfolk Giant.

Propagation of virus-free raspberry plants.

As there were only a few plants of each variety and as the normal means of propagation (division of stools and transplantation of suckers) was slow, special methods of rapid propagation were adopted in order to increase the stocks of virus-free plants to allow of their distribution to commercial growers.

The technique of propagation used was essentially that described by Hudson (1954) and Williams and Hudson (1956). Mother plants, freed from virus by heat treatment, were used to provide annual crops of root cuttings.

In early December the season's cane growth was cut off a few inches above soil level, the contents of the boxes dug out and most of the root system removed from the canes. The canes were then replanted in fresh potting compost to provide root material for the following year. Most of the fine fibrous roots were discarded and the larger roots cut into pieces 4-6 in. long, placed in seed trays half-filled with soil and covered with a 1-in. layer of soil. These were stored in the gauze house until the third week of January when they were brought into a heated glasshouse with a minimum night temperature of 55-60° F. (13-15·5° C.). In about 10-14 days, shoots began to appear above soil level and continued to do so for two or three weeks. These were cut off below soil level and lined out in a propagating case for rooting in a mixture of equal parts sand and peat, at a temperature of about 65° F. Rooting began in about 10-14 days and the young plants were fit for potting into 3-in. pots about two to three weeks after the shoot cuttings were made.

By this means, large numbers of plants can be raised : for example, in 1958/59 the roots from ten boxes of parent plants of Malling Jewel produced more than 3,500 shoots. Losses in the propagating pit were small and varied from one variety to another. Malling Jewel and Lloyd George rooted readily, but Norfolk Giant and Burnetholm Seedling were more difficult and more cuttings of these two varieties died at an early stage.

The young plants were given artificial light from 400-w. mercury vapour lamps for 17 hours daily, to encourage good growth of roots and shoots. They usually required repotting by mid-March, and were than transplanted to 3½-in. wide-based " whale-hide " pots containing John Innes potting compost no. 2 or 3. John Innes compost no. 4 has been tried but this gave rather too soft growth which was liable to damage when the plants were put out in the field. The young plants were gradually hardened off and planted out in the field, in late April to early May, to establish a cane nursery, the crop from which was dug in the autumn of the following year.

The technique described gives extremely uniform planting material which grows well during the first season. The plants are spaced at 1½ ft. in rows 6 ft. apart. Different varieties are planted in blocks, end to end, separated by a strip of fallow 8 ft. wide. Where blocks are planted side by side these must be separated by a strip of clean-cultivated land at least 8 ft. wide to prevent intermingling of roots and young canes. When only one crop of cane is dug from a cane nursery this separation is adequate but, when it is cropped for several years, beds of different varieties must be separated by 15-16 ft. of clean land.

It is important that the young plants be kept free from weeds and allowed to grow without check and with minimum disturbance to the developing root system. Hand hoeing between the plants and mechanical cultivation between the rows is necessary throughout the first growing season. During the second summer fewer

cultivations are necessary as good cane growth smothers most of the annual weeds. The application of one of the newer persistent herbicides, simazine for example, is likely to reduce still further the number of cultivations (Wood and Sutherland, 1958, 1960). The cane nurseries are sprayed at 3-4 week intervals with a systemic insecticide, to control aphids and minimize the spread of viruses.

During the first winter the parent plants must be dug out, otherwise they develop into stools which depress the production of young canes and may produce fruit, seedlings from which would contaminate the stock. This is done by thrusting a spade three or four times into the ground close around each plant so as to leave as much as possible of the root system intact. The following spring, suckers are produced by the roots left in the ground and these develop into canes, with good, fibrous root systems, which are harvested in the autumn, usually during November. Varieties differ in productiveness : Lloyd George, Malling Exploit and Malling Promise are prolific and have given about 10-15 times the number of plants planted, whereas others, such as Malling Jewel, Malling Enterprise and Norfolk Giant have yielded only about 6-10 times the original number of plants.

SUMMARY.

Raspberry plants were freed from infection by some aphid-borne viruses by exposure for 2-3 weeks at temperatures around 35° C. More cures were effected with Norfolk Giant and Malling Jewel than with Lloyd George and Malling Promise, and the results suggest that aphid-borne raspberry viruses differ in ability to multiply in plants at high temperature. The methods used to propagate virus-free plants are described.

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OBSERVATIONS ON THE SEASONAL TRENDS IN THE GROWTH OF THE LEAVES AND FRUIT OF GLASSHOUSE TOMATO PLANTS, CONSIDERED IN RELATION TO LIGHT DURATION AND PLANT AGE

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In previous papers in this series (Cooper, 1958, 1959a and 1959b) trends in the growth of the roots, shoots, leaves and fruit of the tomato were described, and possible relations with the time of the year and the age of the plant were discussed. To obtain further information about these relations it was thought desirable to study the development of plants of different ages at the same time of the year and the development of plants of similar ages at different times of the year.

Methods.

Over a period of twelve months seed of the Potentate variety was sown at intervals of 40 days and data on leaf growth were collected over an unbroken period of twenty months covering part of 1957, the whole of 1958 and part of 1959. The dates of sowing were as follows: 27th Oct., 6th Dec. 1957, 15th Jan., 24th Feb., 5th April, 15th May, 24th June, 3rd Aug. and 12th Sept. 1958.

The seed was sown in soil blocks, one seed per block, and germinated at 70° F. Within a few days of germination five seedlings of identical height and cotyledon length were selected and planted 6 ft. apart in rows, also 6 ft. apart, running east-west across a vinery-type glasshouse, starting at the north end. This systematic layout was used in preference to a randomized one for the following reasons: firstly, it had been concluded from previous work that the seasonal trends to be studied were largely independent of differences in cultural treatment, even including differences in air temperature and soil conditions between different locations and different seasons; consequently it was felt that positional differences in such factors within a glasshouse would not have a marked effect on the phenomena to be studied. Secondly, it was believed that light was the most likely environmental factor to be determining the seasonal trends. Thirdly, for practical reasons, very few experimental plants could be used. Hence it was considered that confounding of the date of sowing with light differences would be minimized by planting systematically from the north end of the glasshouse so that younger and smaller plants would always be to the south of the previous sowing. It was also considered that, with the very few plants that it was practicable to use, the adoption of a randomized layout of plants of very different heights would introduce a large error due to the marked light gradients caused by the consequent shading.

No leaf was removed until the major part of the lamina had lost its green colour and was largely dry and brown. Axillary shoots developing on the main stems were removed as soon as they appeared. Water and fertilizer were applied at weekly intervals from planting, in quantities which it was hoped were sufficiently in excess of requirements to be non-limiting to growth, viz. 20 gallons of water and 3 oz. Nitro-chalk and a proprietary potash-phosphate fertilizer per plant.

Measurements of leaf length from axil to tip and of the diameter of each fruit were made at weekly intervals from November 1957 to June 1959. The cube of the radius was used as an estimate of the volume of each fruit, and is shown as such throughout this paper. As an estimate of the weekly rate of fruit volume production the following equation was used:

$$P = (a_2 + b_2) - (a_1 + b_1)$$

where P = the weekly rate of fruit swelling
a = the fruit volume present on the plant
b = the accumulated total of fruit volume picked
1 = first week under consideration
2 = second week under consideration.

Leaf length was used as an estimate of leaf area as discussed in an earlier paper (Cooper, 1958). The weekly rate of leaf length production (P) was obtained from the foregoing equation by substituting " leaf length " for " fruit volume ".

Results.

Trends in total leaf length and in fruit volume present.

The total leaf length and fruit volume present on the plant increased until maxima were reached. The ages at which these maxima were attained are shown in Table I as the number of days from sowing. It can be seen that the ages were greater for " winter " (Sept.-Jan.) than for " summer " sowings (Feb.-Aug.). The sizes of the maxima also were greater for winter sowings. Thus the periods of increasing leaf area and increasing fruit volume are longer with winter than with summer sowings, and the plants also develop a larger maximal leaf area and a larger maximal fruit volume.

Table I.

Maximal total leaf length and fruit volume present on the plant.

Sowing	Oct.	Dec.	Jan.	Feb.	Apr.	May	June	Aug.	Sept.
Age at leaf length maximum (days)	325	271	231	191	123	181	197	185	215
Maximal leaf length (cm.)	2,443	2,268	2,406	1,871	1,510	1,716	1,728	1,731	1,983
Age at fruit volume maximum (days)	220	173	161	156	130	139	120	115	250
Maximal fruit volume (c.c.)	2,022	2,687	1,680	1,570	1,760	1,249	978	766	1,474

Trends in leaf length production and fruit volume production.

The variation within the five plants in each sowing was such that conclusions based on data from single plants did not differ materially from conclusions based on the means of five plants.

To cover the longest possible time span, the data from the longest-lived plant in each sowing have been used in Fig. 1, where the weekly rates of leaf length production and fruit volume production are plotted against the time of the year. All sowings, except that for September, had a similar basic leaf growth pattern: first, a primary stage of growth in which there was a fairly rapid rise to a maximal rate, then a decline to a secondary stage in which the growth rate was maintained at a relatively low level. The September sowing showed merely a rise in growth rate to the relatively low level of the secondary stage, which it maintained. It appeared to enter directly into the secondary stage of growth without passing through the primary. The maximal rates of leaf growth reached are given in Table II for the means of five plants.

Table II.

Mean maximal rates of leaf length production (cm. per week) and leaf length present at attainment of maximal rate (cm.).

Sowing	Oct.	Dec.	Jan.	Feb.	Apr.	May	June	Aug.	Sept.
Maximal rate	166	166	170	172	174	172	177	194	97
Leaf length present	1,056	796	589	605	575	538	405	504	394

The maximal rates were fairly similar for the different sowing dates from October to June, ranging from 166 to 177 cm. per week. There was an increase to 194 cm. per week for the sowing of 3rd August, but the major effect was the marked reduction in that of 12th September. Table II also shows that there is no relation between the leaf area present on the plant at the time the maximum is reached and the size of the maximum.

The swelling of the first ovaries, indicated in Fig. 1 by the letter F, coincided in all sowings with the period of maximal leaf length production, irrespective of the age of the plant, the time of the year at which the period of maximal leaf length production was reached, or the magnitude of the maximal rate attained. There would thus appear to be a relation between leaf growth and the start of fruiting. This is not a relation with the attainment of a given rate of leaf length production, however, since Fig. 1 shows that the rate attained by the September sowing when fruiting began was only approximately half that attained by the other sowings.

It was found by Fisher (1955) that, in soybean, fruiting began when a certain ratio of immature to mature leaf area was reached. Fig. 2 suggests that this may also be true of the tomato, but that fruiting may begin at one of two ratios according as the day is longer or shorter than the night. In Fig. 2 the date at which each sowing began fruiting is shown. Between the spring and autumn equinoxes this was when the ratio of immature to mature leaf length approximated to 19 : 1 (indicated by the upper broken line); between the autumn and spring equinoxes it was when the ratio was approximately 4 : 1 (indicated by the lower broken line). Fig. 1 shows that in all sowings, when the first ovaries began to swell, the steadily increasing rate of leaf growth was checked and there was no further increase in the weekly rate of leaf length production. Generally the start of fruiting was followed

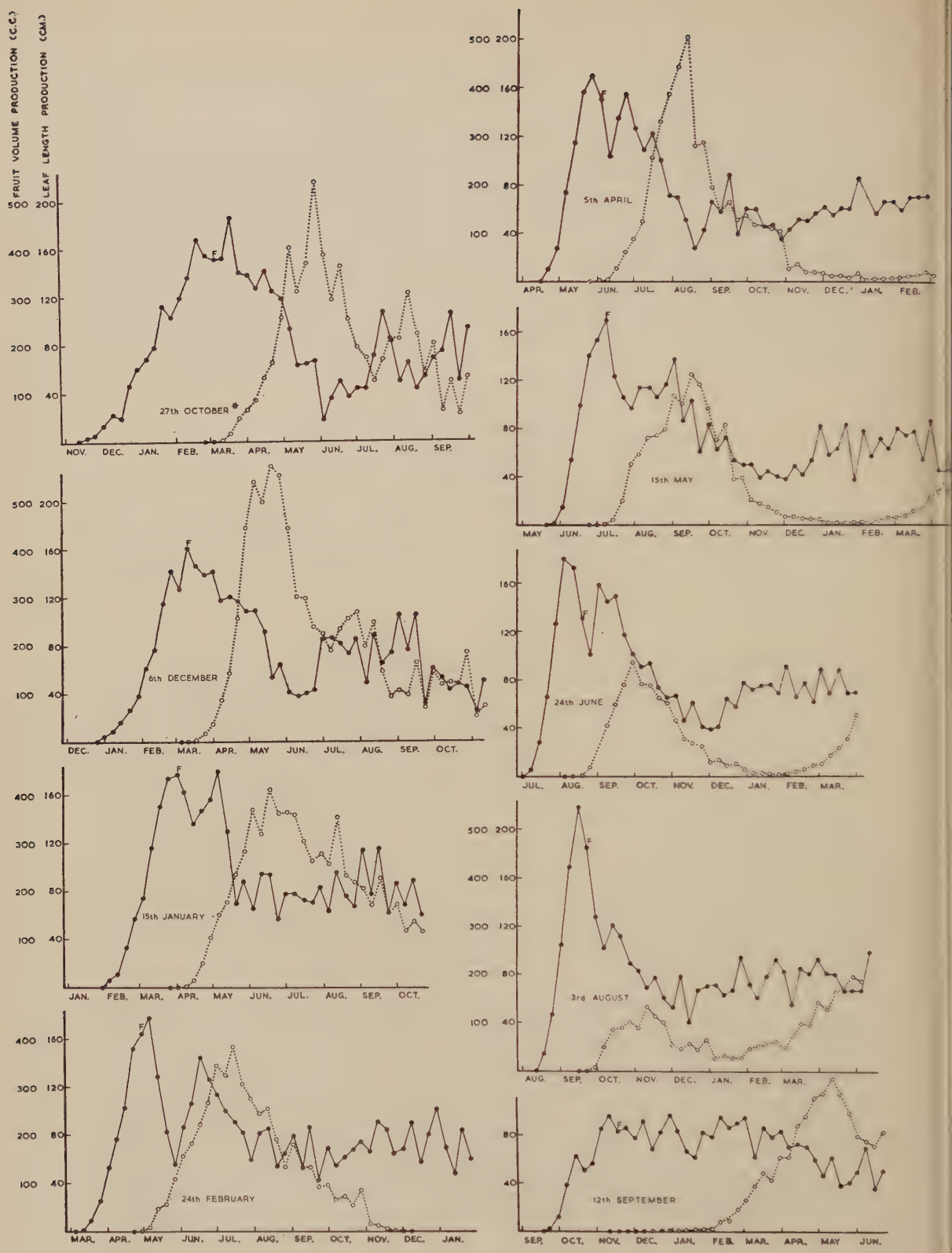
FRUIT VOLUME PRODUCTION (C.C.)
LEAF LENGTH PRODUCTION (CM.)
27th OCTOBER *
NOV. DEC. JAN. FEB. MAR. APR. MAY JUN. JUL. AUG. SEP.
5th APRIL
APR. MAY JUN. JUL. AUG. SEP. OCT. NOV. DEC. JAN. FEB.
15th MAY
MAY JUN. JUL. AUG. SEP. OCT. NOV DEC. JAN. FEB. MAR.
6th DECEMBER
DEC. JAN. FEB. MAR. APR. MAY JUN. JUL. AUG. SEP. OCT.
24th JUNE
JUL. AUG. SEP. OCT. NOV. DEC. JAN. FEB. MAR.
15th JANUARY
JAN. FEB. MAR. APR. MAY JUN. JUL. AUG. SEP. OCT.
3rd AUGUST
AUG. SEP. OCT. NOV. DEC. JAN. FEB. MAR.
24th FEBRUARY
MAR. APR. MAY JUN. JUL. AUG. SEP. OCT. NOV. DEC. JAN.
12th SEPTEMBER
SEP. OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY JUN.

FIG. 1.

Daily rate of leaf length production (continuous line) and fruit volume production (dotted line).

* Date of sowing; F, beginning of swelling of first ovaries.

by a rapid rise in the weekly rate of fruit production and there was an associated decline in leaf length production. However, the September sowing, which began fruiting in early November, was aberrant in that, although each ovary began to swell, this swelling was largely arrested and fruit development was very slow. Consequently, during November, December and January the total fruit volume on the plant was extremely small. None the less, there was a similar check to the rise in leaf length production to that recorded for the other sowings.

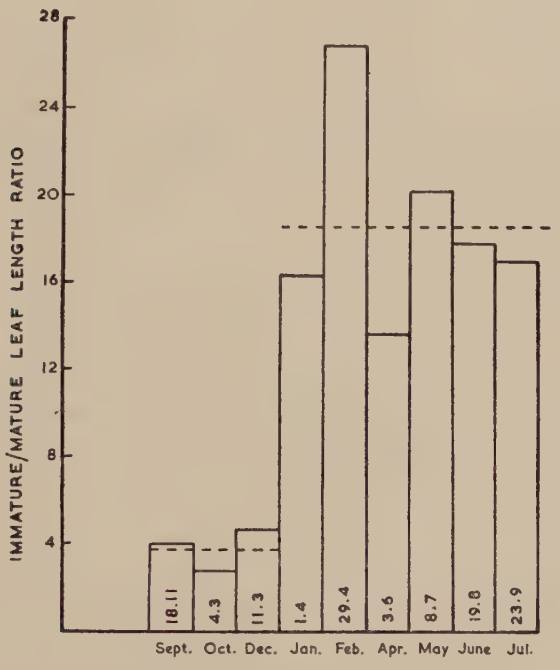

Fig. 2.
Relation of immature to mature leaf length at start of fruiting. Figures give dates at which fruiting began. For broken lines, see p. 57.

This marked arrest of ovary swelling during November, December and January was also recorded on all sowings made from February to September. Fruit volume production invariably declined to a level approaching zero during the period November-January, although the plants were of very different ages. They were also bearing differing volumes of fruit, as can be seen from Table III where the mean weekly fruit volume present per plant is shown for the months of November, December and January.

Fig. 1 shows that, for all sowings, the weekly rate of fruit volume production increased until a maximal rate was reached, after which there was a sudden marked decline in production. This decline was independent of the age of the plant or the time of the year. It was, however, associated with the attaining of a minimal ratio of leaf area to fruit volume present on the plant. This ratio was constant for sowings (October to April) that began fruiting between the shortest day and the

TABLE III.

Mean weekly fruit volume per plant, as cube of the radius (c.c.), present on the plant.

Sowing	Feb.	Apr.	May	June	Aug.	Sept.
Fruit volume in:						
November ..	221·5	230·9	314·3	578·7	657·4	0·1
December ..	24·1	87·6	133·1	227·7	459·5	0·4
January ..	0·4	47·4	36·4	61·5	281·3	9·7

longest day. The ratio was higher for sowings (May to September) that began fruiting between the longest day and the shortest, and the ratio tended to increase as the sowing date approached the shortest day. These data are shown in Table IV.

TABLE IV.

Leaf length/fruit volume ratio at maximal rate of fruit volume production.

Sowing	Oct.	Dec.	Jan.	Feb.	Apr.	May	June	Aug.	Sept.
Date of start of fruiting ..	4th Mar.	11th Mar.	1st Apr.	29th Apr.	3rd June	8th July	19th Aug.	23rd Sept.	18th Nov.
Leaf length/fruit volume (cm./c.c.)	1 : 1	1 : 1	1 : 1	1 : 1	1 : 1	2 : 1	3 : 1	4 : 1	4 : 1

Once these minimal ratios were reached, the weekly rate of fruit volume production began to decline, as shown in Fig. 1. Throughout the remainder of the life of the plants the weekly rates of leaf length production and fruit volume production were inter-related in such a way that there was little marked departure from the minimal leaf area/fruit volume ratios, with one exception. Because of the extremely low rate of fruit volume production over the period November-January, and because leaf length production was not correspondingly reduced, the leaf length/fruit volume ratio rose rapidly until about the end of January, when an equally rapid decrease in the ratio occurred as fruit development began again.

These phenomena are illustrated in Fig. 3(a). The ratios for the first few weeks of fruiting in each sowing have not been shown because of their very large values. In Fig. 3(b) a composite curve has been constructed from the data of Fig. 3(a) to show the effect of the time of the year on the leaf area/fruit volume ratio for mature fruiting plants, i.e. plants that had attained their maximal rate of fruit production.

In Fig. 1 the data for leaf growth obtained from the September sowing appeared to be aberrant relative to those obtained from the others. When leaf growth is considered in terms of leaf area/fruit volume in relation to time of year as in Fig. 3, it is seen that the seasonal pattern of development of the September sowing conforms with that of the others.

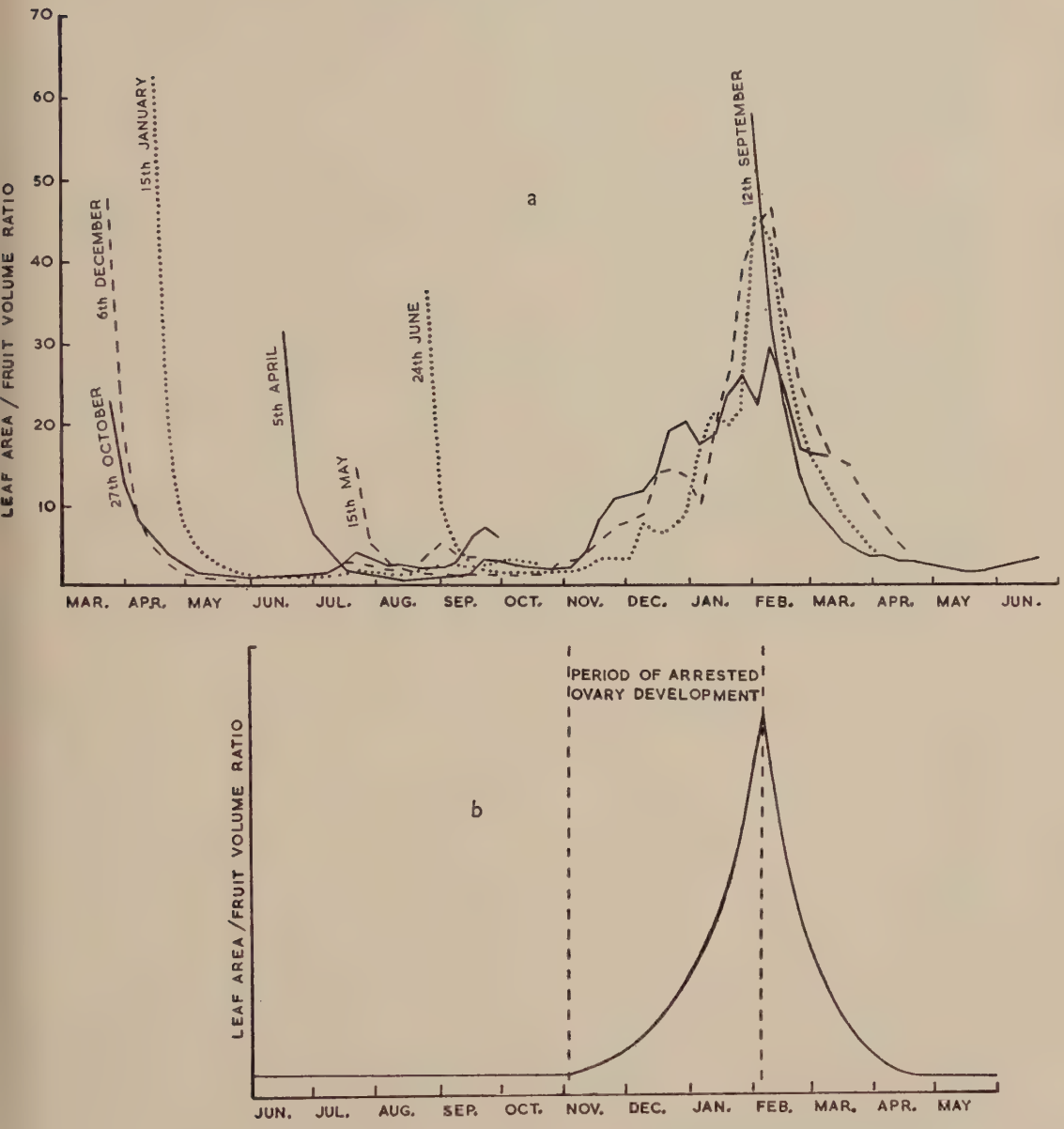

Fig. 3.
Variation of leaf area/fruit volume ratio throughout the year. (a) records of 7 sowings on different dates; (b) composite curve for all sowings.

Time taken to attain maximal rates of leaf length and fruit volume production.

In Table V the time taken to attain the maximal rate of leaf length production (i.e. the start of ovary swelling) is shown for each sowing as the number of days from sowing. The length of this period varied regularly through the season, there being a decrease with progress from the winter to the summer sowings.

TABLE V.

Plant age on attainment of maximal rate of leaf length production.

Sowing	Oct.	Dec.	Jan.	Feb.	Apr.	May	June	Aug.	Sept.
Age (days from sowing) ..	114	95	69	64	52	47	42	44	60

In Fig. 4 the number of days to attainment of the maximal rate of leaf length production (coincident with start of fruiting, see F in Fig. 1) are shown plotted against the mean night lengths from germination to the attainment of the maximal rate. The data for October to January sowings fit the regression line $x = 0{\cdot}5y - 287{\cdot}0$ quite closely, while those for the remainder fit the regression line $x = 0{\cdot}5y + 25{\cdot}0$. If the threshold light intensity for these two relations to operate is assumed to lie between the intensities at dawn and sunrise and to be close to the light intensity of dawn, it can be seen from Fig. 4 (where the dusk-dawn night lengths have been used) that the change from the one relation to the other occurs at the condition of equal day and night.

The data presented can thus be explained by postulating an effect of darkness (or light) on the age at which the maximal rate of production of leaf area is reached

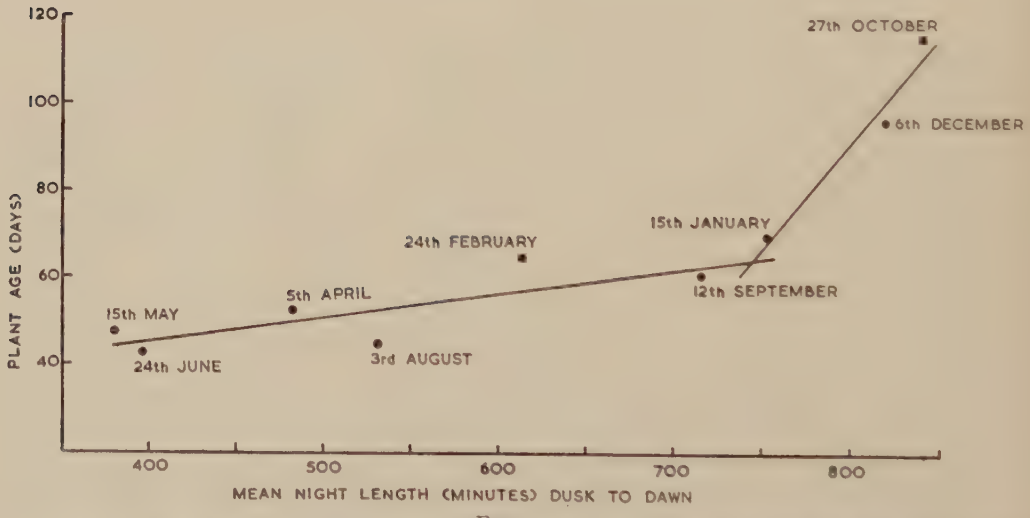

FIG. 4.

Relation between plant age on attaining maximal rate of leaf length production and the mean night length during that period.

and ovary swelling begins; the longer the night length the greater the age, with the effect of unit change in night length being greater at night lengths of more than twelve hours than at night lengths of less than twelve hours.

Once ovary swelling began, the time taken to attain the maximal rate of fruit volume production (i.e. minimal leaf area/fruit volume ratio) approximated to a constant of 12 weeks (indicated by the line XX in Fig. 5, left) for plants sown from October to May. The September sowing departed markedly from this constant but, if the period of arrested ovary development which it experienced is not counted, it no longer deviates from the constant. Thus only two sowings (June and August) deviate from the constant. It could be argued that this was due to unknown positional effects within the glasshouse. The conformity of data on leaf and fruit growth already considered from these two sowings lends little support to such an hypothesis, however. Fig. 5 (right) shows that the total fruit production of the June and August sowings is in conformity with a general seasonal trend. In this graph the mean volume of fruit per plant picked during a period of 280 days from sowing is shown. It can be seen that there is a well defined seasonal trend in yield. The nearer to the shortest day that germination occurs the greater is the total yield, the nearer to the longest day the smaller the yield. Knowledge of the existence of such a relation is of practical value.

A further subject of practical interest is the time elapsing from sowing to the ripening of the first fruit. Table VI, which gives the length of this period for each sowing, shows that ripening begins earliest in the life of the plant when sowings are made in April-June and latest when they are made in September and October. Sowings made in intermediate months behave intermediately.

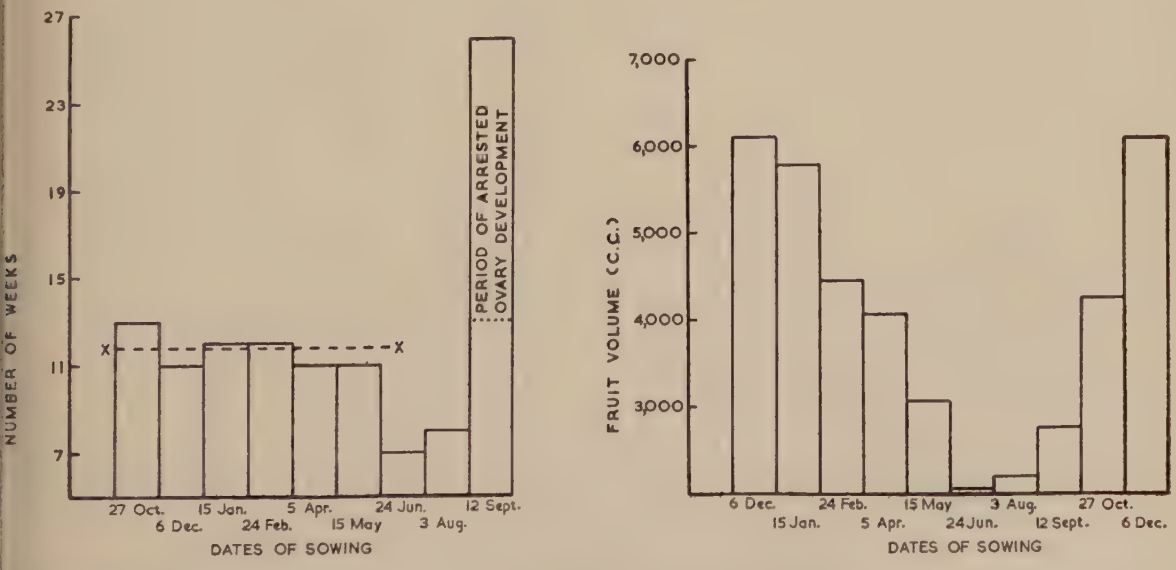

Fig. 5.
(*Left*) Number of weeks from start of fruiting to maximal rate of fruit volume production. (*Right*) Total yield.

TABLE VI.

Plant age at ripening of first fruit.

Sowing	Oct.	Dec.	Jan.	Feb.	Apr.	May	June	Aug.	Sept.
Age (days from sowing) ..	192	159	137	121	102	106	105	121	179

Duration of growth of individual leaves.

The time taken by individual leaves to attain their mature size was not constant, the period of growth varying from 22 to 71 days. In Table VII are given the correlation coefficients (each based on 300 to 400 leaves) for the duration of this growth period and the length of the day (dawn to dusk) at the time the leaves appeared. A leaf was judged to have appeared when it reached a length of 5 mm. All these coefficients are negative and significant at the 0·01 level of probability.

The data thus suggest the possibility that the duration of the growth of individual leaves is influenced by the duration of light (or darkness) during growth—the longer the day the shorter the growth period. It is of interest that plants that made much of their development (particularly their early development) during the winter months gave smaller correlation coefficients than did sowings made in the summer.

TABLE VII.

Correlation coefficients for duration of growth of leaves and day-length at time of appearance.

Sowing	Oct.	Dec.	Jan.	Feb.	Apr.	May	June	Aug.	Sept.
	−0·6	−0·5	−0·7	−0·8	−0·8	−0·9	−0·8	−0·8	−0·6

The above method of using the day-length at leaf appearance as an estimate of the mean day-length over the growth period of a leaf is open to the criticism that it provides a poor estimate, the duration of the growth period of leaves not being a constant and some leaves appearing when the day-length is increasing, others when it is decreasing. Because it reduces the necessary computation it does, however, enable a very large number of leaves (approximately 3,000 in the present work) to be used in testing the relationships.

As a measure of the validity of the method, the mean day-lengths of the growth periods of thirty leaves selected at random from all the sowings have been determined and correlated with the duration of their growth periods. The correlation coefficient so obtained was −0·7 and it was significant at the 0·01 level of probability, confirming the validity of the simpler method.

To provide a further test of the relation of growth period to day-length, leaves that had the same growth period were grouped together irrespective of the different sowing dates of the plants. When there were more than ten leaves with the same

growth period, the mean day-length at which the leaves appeared was determined. These data have been plotted in Fig. 6.

Two regression lines have been fitted:

$$\text{(i)}\quad x = 85{\cdot}8 - 0{\cdot}06y$$
$$\text{(ii)}\quad x = 251{\cdot}7 - 0{\cdot}3y$$

the first relation holding for day-lengths longer than approximately $10\frac{1}{2}$ hours (dawn to dusk), the second for shorter day-lengths.

These findings suggest that the rate of change in the duration of leaf growth relative to the rate of change in the duration of light is about five times greater at day-lengths below $10\frac{1}{2}$ hours at the time of appearance of the leaves than in longer days, since the ratio of the regression coefficients is 0·3 : 0·06.

Mature leaf length.

All the sowings showed a similar pattern of change in mature leaf length. The latter increased steadily the higher up the plant the leaf was situated, until a maximum was reached. This maximum was not related to leaf position *per se*, but varied with the sowing date. Table VIII shows that winter sowings (October to February) produced leaves of maximal size at higher leaf positions than did summer sowings (April to September). In winter sowings the position for maximal leaf size was highest in the October sowing and decreased as the sowing date progressed towards January, whereas there was no trend in the summer sowings, the leaf position at

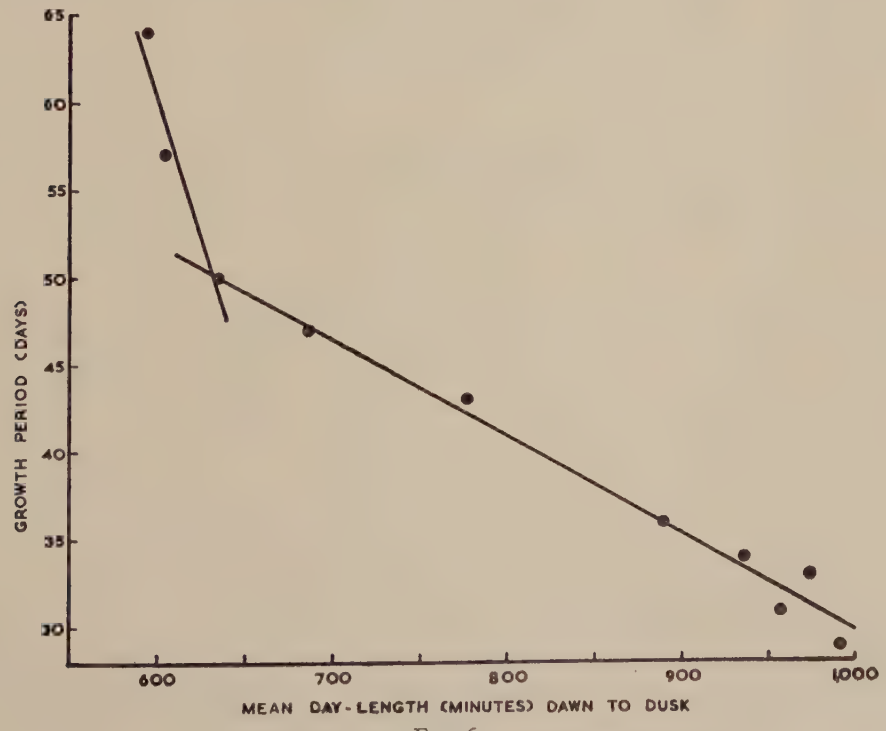

Fig. 6.
Relation between growth period of leaves and day-length.

which maximal mature length was attained being constant at leaf 7-8. The results obtained with the winter sowings substantiate the results of more limited work previously reported by Cooper (1959b).

TABLE VIII.
Leaf position and plant age at appearance of longest leaf.

Sowing	Oct.	Dec.	Jan.	Feb.	Apr.	May	June	Aug.	Sept.
Position of longest leaf ..	18	15	10	10	7	8	8	8	8
Plant age at appearance of longest leaf (days) ..	83	68	56	58	32	34	29	31	33

The age of the plant at which the longest leaf appeared also varied in a similar manner, and the age was virtually constant for sowings from April to September, ranging from 29 to 34 days. The mid-points of the 40-day sowing interval between 24th February and 5th April, and between 12th September and 27th October provide an approximate estimate of the dates of germination between which the constant condition of age and leaf position prevails. These dates are 16th March and 2nd October. On these dates day-lengths from dawn to dusk are 12 hours 59 minutes and 12 hours 45 minutes respectively and from sunrise to sunset 11 hours 54 minutes and 11 hours 35 minutes. Thus it is possible that the limits may be defined by the condition of equal light and dark if the assumption is made that the threshold light intensity lies between the intensity of dawn and that of sunrise.

Number of leaves between inflorescences.

In Table IX the mean number of leaves to the first inflorescence, and between the first and second inflorescences, are shown. Fewer leaves were produced before flowering in the winter sowings (October to February) than in the summer ones (April to September).

TABLE IX.
Number of leaves between inflorescences.

Sowing	Oct.	Dec.	Jan.	Feb.	Apr.	May	June	Aug.	Sept.
Ground to 1st inflorescence ..	6·0	7·0	7·0	6·6	7·6	7·6	8·5	8·0	8·2
1st to 2nd inflorescence ..	6·2	5·2	5·2	4·8	3·6	3·6	3·0	3·0	3·4
Ground to 2nd inflorescence ..	12·2	12·2	12·2	11·4	11·2	11·2	11·5	11·0	11·6

The number of leaves between the first and second inflorescence was negatively correlated with the number of leaves to the first inflorescence, being fewer in the summer than in the winter sowings. Thus the total number of leaves to the second inflorescence was constant (11 to 12) for all sowings. This suggests that the number of leaves between the first and second inflorescences may be dependent on the number of leaves to the first inflorescence. The mean number of leaves between subsequent inflorescences was constant at three leaves for all sowings.

DISCUSSION.

From the data presented it can be concluded that the seasonal pattern of development of the leaves and the fruit of the tomato appears to be determined by at least two factors: firstly, by an inter-relation between leaf development and fruit development, and secondly, by changes in light duration.

Salter (1958) drew the conclusion that fruiting caused a reduction in vegetative growth, and that this reduction was the result of the ability of fruit developing on plants grown under sub-optimal conditions to monopolize the food resources of the plant. McCollum (1934) suggested that fruits secrete a growth-inhibiting substance which retards vegetative growth.

In the present work the September sowing began to fruit during November, but ovary development was arrested at an early stage and remained so until the following February. The volume and number of fruit present on the plant was extremely small and presumably provided little competition for food resources, yet there was an immediate check in leaf length production within a few days of the start of fruiting. This immediate check was also observed in the other sowings.

Further evidence that does not support Salter's view was provided by the virtual cessation of fruit volume production during November, December and January in plants which began fruiting before this period. Since this phenomenon was associated with a specific time of the year and was independent of fruit load, leaf area and age of the plant, it is reasonable to assume that the glasshouse environment during these months was sub-optimal for tomato development. However, fruit development was retarded more than leaf development, and the leaf area/fruit volume ratio rose rapidly. Presumably, any monopolization of food reserves by the fruit does not extend to all food substances, or else some substance, the production of which was adversely affected, is required for fruit development but not for leaf growth.

The data on leaf area/fruit volume ratio suggest that in the tomato a balance is maintained between fruit and leaf growth. When fruiting begins there is a rapid decrease in the leaf area/fruit volume ratio until a minimal value is attained. Once this has been established it is maintained throughout the remainder of the life of the plant. This phenomenon suggests, not the existence of competition between leaf growth and fruit growth, but rather the existence of a regulatory mechanism that maintains a balance between the two. Knowledge of such a balance would be of practical importance because of the commercial practice of removing lower leaves; this, presumably, would adversely affect fruiting if a regulatory mechanism exists within the plant for maintaining a balance between leaf and fruit growth, as the ratio could be restored only by a reduction in the rate of ovary swelling relative to leaf growth.

From the data presented it would appear that, once attained, the minimal ratio is maintained until arrested ovary development occurs during November, December and January; then the ratio rises, and subsequently falls as active ovary development begins again in February. Thus the seasonal trends in fruit and leaf growth appear to be determined by an inter-relation between them, and also by some factor of the November-January environment that disturbs this inter-relation by arresting ovary swelling *when the plant is grown with completely unrestricted root run from germination onwards.*

The seasonal trends in leaf number up to the second inflorescence appear to be

similarly determined both by an internal regulatory mechanism and by the environment. In the winter months fewer leaves were produced before initiation of the first inflorescence, but throughout the year a regulatory mechanism appeared to operate so that the number of leaves between the first and second inflorescence was negatively correlated with the number of leaves to the first inflorescence, and hence the total number of leaves to the second inflorescence was maintained constant irrespective of seasonal changes in environment. This phenomenon is of practical importance where attempts are being made to influence early yield.

When the data presented are considered as a whole, patterns of development can be seen that suggest that tomato development is affected by changes in light duration. The ratio of immature to mature leaf area at which fruiting began was high or low according as the plant, prior to fruiting, was growing at day-lengths of more or less than twelve hours. The marked, similar changes in this ratio between the December and January sowings and between the August and September sowings suggest that there is a fairly immediate and marked response by the plant to a change from a day-length less than twelve hours to one of more than twelve hours, and *vice versa*.

When the start of fruiting is considered in relation to the age of the plant, it can be seen that the shorter the day-length at which the plant is growing the older the plant is at the start of fruiting. There is, however, a marked change in the relation at the condition of equal light and dark, unit change in day-length having a much greater effect at day-lengths of less than twelve hours. There is also a significant negative correlation between the day-length at which a leaf is growing and the duration of its period of growth.

SUMMARY.

Seed of the Potentate variety of tomato was sown at 40-day intervals and weekly measurements of the length of every leaf and the diameter of every fruit were made to provide estimates of leaf area and fruit volume from germination until each plant reached an advanced age approaching twelve months.

It was found that plants sown in the winter months (October-February) had a longer period of increasing leaf area and attained a larger total maximal leaf area than plants sown in the summer months (April-September).

The pattern of leaf area production was similar for all sowings except one. The weekly rate increased until a maximum was reached and then declined to a relatively low level which was maintained. The start of the decline from the maximum coincided in all sowings with the swelling of the first ovaries. The first ovaries began to swell at one of two immature/mature leaf area ratios, namely at a ratio of 19 : 1 when the duration of light exceeded that of darkness, and at a ratio of 4 : 1 when it did not. The age at which these ratios were reached was negatively correlated with the day-length, the effect of unit change in day-length being greater at day-lengths of less than 12 hours than at day-lengths of more than 12 hours.

Arrested ovary development was shown during November, December and January by all plants, irrespective of the age of the plant or the volume of fruit present on the plant at the beginning of the period of arrested development.

The pattern of development of fruit volume production was similar for all sowings. The weekly rate increased until a maximum was reached and the attainment of this maximum coincided in all sowings with the attainment of a minimal

leaf area/fruit volume ratio. This minimal ratio was subsequently maintained until the start of the period of arrested ovary development. During this period leaf growth was not so adversely affected and consequently the ratio rose rapidly.

A seasonal trend was observed in the total yield of fruit over a period of 280 days from sowing. The closer to the shortest day that germination occurred the greater was the yield, the nearer to the longest day the smaller the yield.

At day-lengths of more than 12 hours the largest leaf on the plant was always the 7th or 8th, and it was produced at an age of 29 to 34 days from sowing. At shorter day-lengths the largest leaf was produced at later ages and higher positions, the age and position varying with the sowing date, being greatest for the October and December sowings.

Fewer leaves were produced before flowering in the winter months than in the summer, but, conversely, there were more leaves between the 1st and 2nd inflorescences in the winter than in the summer. The number of leaves between the 1st and 2nd inflorescences depended on the number of leaves produced before the first floral initials were formed, since the total leaf number to the second inflorescence was constant throughout the year at 11 to 12.

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BOOK REVIEWS

SOIL STERILIZATION. Ministry of Agriculture, Fisheries and Food Bulletin No. 22. Fifth edition. (London : H.M. Stationery Office. 1959. Pp. 49, illus. Price 4s.)

The fifth edition of this bulletin has been completely revised and rewritten. There is now a valuable discussion of the principles underlying certain features of steam sterilization, such as breaking up the soil, rate of steaming and the relative unimportance of high pressures, which will lead to a better understanding of this important soil treatment. A comprehensive summary of the major practical points to bear in mind is provided in Appendix I.

Where steam is not available and the quantity of soil is too large for sterilization by means of electricity, portable oil-fired rotating drum sterilizers may be used if pests and diseases necessitate measures beyond the scope of soil chemicals. This does not mean that such chemicals are unimportant ; they are useful alternatives to steam, and are comparatively cheap.

The importance of hygiene is rightly emphasized, especially in view of the expense involved in all methods of soil sterilization.

This excellent publication will appeal to all those interested in improving the culture of plants and the productivity of glasshouse soils.

M.M.M.

SOILS AND MANURES FOR VEGETABLES. Ministry of Agriculture, Fisheries and Food Bulletin No. 71. Third edition. (London : H.M. Stationery Office. 1959. Pp. 78. Price 5s.)

This, the third edition of the bulletin, has been completely rewritten and is in effect a new publication. It is a comprehensive work dealing with all the major aspects of vegetable nutrition.

Vegetables are grown on a wide range of soils and the concept of market garden soils as a special class is less marked than in the past when large supplies of farmyard manure were available. The advantages and limitations of different types of soils and the methods used in the assessment of their suitability for vegetable growing are clearly set out and there is an underlying theme of the importance of the selection of crops to suit any particular soil type.

The role of the major and minor elements in crop nutrition is described and the properties of most of the fertilizer materials available in the United Kingdom are explained.

The use of bulky organic materials and organic waste products is discussed but, in the manurial recommendations in the latter part of the book, insufficient allowance is made for the nutrients supplied by farmyard manure. On most soils, if it is applied at 20 tons per acre, there is no need to supply phosphate and potash in the fertilizer mixture.

The least satisfactory part of the bulletin is the section dealing with the manuring for particular vegetable crops, for, as is clearly stated by the authors, there are few experimental results on which to base their recommendations. In general, they are based on the practice of successful growers and the experience of the officers of the National Agricultural Advisory Service. Whilst most of the programmes suggested seem to be satisfactory, the reviewer is of the opinion that the recommended rates of application of nitrogenous fertilizers are in general too low, and lower than those in widespread use in the Vale of Evesham. In particular, early Primo cabbage and red beet are very responsive to inorganic fertilizers on many soils and the rates of application suggested seem to be inadequate.

The publications committee are to be congratulated in condensing so much useful information into one small and very readable volume which should be of value to the commercial grower and amateur gardener alike.

F.H.

PUBLICATIONS RECEIVED

THE EFFECTS OF POLLUTION ON LIVING MATERIAL. Symposia of the Institute of Biology, No. 8. Edited by W. B. Yapp. (London : Institute of Biology. 1959. Pp. 154, illus. Price 25s.)

MUSHROOM GROWING. Ministry of Agriculture, Fisheries and Food Bulletin No. 34. Seventh edition. (London : H.M. Stationery Office. 1960. Pp. 66, illus. Price 6s.)

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2. Authors of papers containing extensive **numerical observations** should consult the recommendations of the British Association Committee on Biological Measurements, 1927, obtainable from Burlington House, London, W.1, price 6d. Arrangements have been made whereby original data too extensive for complete publication may be deposited at the British Museum (Natural History), London, S.W.7, or with the Royal Society of Edinburgh, 22 George Street, and thus be available for consultation by other workers. Full bibliographical reference to the publication in which the results are summarized must be supplied with the data.

3. Each paper must conclude with a concise and critically correct **summary** of its actual content. It should contain any new or verified constants as well as any other critical data of permanent value but not tables or graphs. Any organism mentioned should be given its scientific name.

4. Where a paper is of a highly technical nature it should be preceded by a brief **synopsis,** in which its contents are simply and clearly stated for the benefit of non-technical readers.

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10. The suggested **abbreviation** for the title of this publication is *J. hort. Sci.*

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